



The obstetrical dilemma hypothesis: there's life in the old dog yet

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Abstract: The term 'obstetrical dilemma' was coined by Washburn in 1960 to describe the trade-off between selection for a larger birth canal, permitting successful passage of a big-brained human neonate, and the smaller pelvic dimensions required for bipedal locomotion. His suggested solution to these antagonistic pressures was to give birth prematurely, explaining the unusual degree of neurological and physical immaturity, or secondary altriciality, observed in human infants. This proposed trade-off has traditionally been offered as the predominant evolutionary explanation for why human childbirth is so challenging, and inherently risky, compared to that of other primates. This perceived difficulty is likely due to the tight fit of fetal to maternal pelvic dimensions along with the convoluted shape of the birth canal and a comparatively low degree of ligamentous flexibility. Although the ideas combined under the obstetrical dilemma hypothesis originated almost a century ago, they have received renewed attention and empirical scrutiny in the last decade, with some researchers advocating complete rejection of the hypothesis and its assumptions. However, the hypothesis is complex because it presently captures several, mutually non-exclusive ideas: (i) there is an evolutionary trade-off resulting from opposing selection pressures on the pelvis; (ii) selection favouring a narrow pelvis specifically derives from bipedalism; (iii) human neonates are secondarily altricial because they are born relatively immature to ensure that they fit through the maternal bony pelvis; (iv) as a corollary to the asymmetric selection pressure for a spacious birth canal in females, humans evolved pronounced sexual dimorphism of pelvic shape. Recently, the hypothesis has been challenged on both empirical and theoretical grounds. Here, we appraise the original ideas captured under the 'obstetrical dilemma' and their subsequent evolution. We also evaluate complementary and alternative explanations for a tight fetopelvic fit and obstructed labour, including ecological factors related to nutrition and thermoregulation, constraints imposed by the stability of the pelvic floor or by maternal and fetal metabolism, the energetics of bipedalism, and variability in pelvic shape. This reveals that human childbirth is affected by a complex combination of evolutionary, ecological, and biocultural factors, which variably constrain maternal pelvic form and fetal growth. Our review demonstrates that it is unwarranted to reject the obstetrical dilemma hypothesis entirely because several of its fundamental assumptions have not been successfully discounted despite claims to the contrary. As such, the obstetrical dilemma remains a tenable hypothesis that can be used productively to guide evolutionary research

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The obstetrical dilemma hypothesis: there's life in the old dog yet

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ABSTRACT

The term ‘obstetrical dilemma’ was coined by Washburn in 1960 to describe the trade-off between selection for a larger birth canal, permitting successful passage of a big-brained human neonate, and the smaller pelvic dimensions required for bipedal locomotion. His suggested solution to these antagonistic pressures was to give birth prematurely, explaining the unusual degree of neurological and physical immaturity, or secondary altriciality, observed in human infants. This proposed trade-off has traditionally been offered as the predominant evolutionary explanation for why human childbirth is so challenging, and inherently risky, compared to that of other primates. This perceived difficulty is likely due to the tight fit of fetal to maternal pelvic dimensions along with the convoluted shape of the birth canal and a comparatively low degree of ligamentous flexibility. Although the ideas combined under the obstetrical dilemma hypothesis originated almost a century ago, they have received renewed attention and empirical scrutiny in the last decade, with some researchers advocating complete rejection of the hypothesis and its assumptions. However, the hypothesis is complex because it presently captures several, mutually non-exclusive ideas: (i) there is an evolutionary trade-off resulting from opposing selection pressures on the pelvis; (ii) selection favouring a narrow pelvis specifically derives from bipedalism; (iii) human neonates are secondarily altricial because they are born relatively immature to ensure that they fit through the maternal bony pelvis; (iv) as a corollary to the asymmetric selection pressure for a spacious birth canal in females, humans evolved pronounced sexual dimorphism of pelvic shape. Recently, the hypothesis has been challenged on both empirical and theoretical grounds. Here, we appraise the original ideas captured under the ‘obstetrical dilemma’ and their subsequent evolution. We also evaluate complementary and alternative explanations for a tight fetopelvic fit and obstructed labour, including ecological factors related to nutrition and thermoregulation, constraints imposed by the stability of the pelvic floor or by maternal and fetal metabolism, the energetics of bipedalism, and variability in pelvic shape. This reveals that human childbirth is affected by a complex combination of evolutionary, ecological, and biocultural factors, which variably constrain maternal pelvic form and fetal growth. Our review demonstrates that it is unwarranted to reject the obstetrical dilemma hypothesis entirely because several of its fundamental assumptions have not been successfully discounted despite claims to the contrary. As such, the obstetrical dilemma remains a tenable hypothesis that can be used productively to guide evolutionary research.

Key words: obstetrical dilemma, bipedalism, secondary altriciality, obstetrics, birth, pelvis, pelvic width, antagonistic selection, sexual dimorphism, human evolution

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CONTENTS

I. Introduction	2
(1) Human birth: a risky business and a tight squeeze	2
(2) The 'Obstetrical Dilemma'	3
II. The birth process	6
III. Birth timing	9
IV. Sexual dimorphism	10
V. Alternative and complementary views to the obstetrical dilemma hypothesis	12
(1) Variability of pelvic shape	12
(2) Energetics of bipedalism	13
(3) Energetics of gestation and growth	15
(4) Thermoregulation	17
(5) Pelvic floor stability	18
(6) Nutrition and phenotypic plasticity	20
VI. Outlook	21
VII. Conclusions	22
VIII. Acknowledgements	22
IX. References	23

I. INTRODUCTION

(1) Human birth: a risky business and a tight squeeze

For modern humans, birth is a remarkably complex process compared to most other mammals. Despite its ubiquity, the birth process presents several hazards for both mother and offspring. Although modern obstetric care has virtually eliminated maternal mortality in developed countries, recent estimates suggest that in some parts of the world the maternal mortality rate still exceeds 1000 per 100000 live births, and the lifetime risk of a woman dying as a result of childbirth is a dramatic 1:15 (WHO *et al.*, 2014).

Historical records also document disturbingly high death rates related to childbirth in much of Europe, persisting until the 1930s (Loudon, 1992, 2000; Chamberlain, 2006). In 18th and 19th-century England, maternal mortality rates of 750–1050 per 100000 live births and 500 per 100000 live births, respectively, have been estimated based on parish records (Loudon, 2000). Similar to developing countries today, part of this high maternal mortality rate may be explained by malnutrition and an associated high prevalence of chronic iron deficiency anaemia that often resulted in death from haemorrhage, together with deficiencies in vitamin D and calcium, which were rampant during industrialisation and which may lead to a contracted pelvis (Wells, 1975; Wells, DeSilva & Stock, 2012). Another important factor were instrumental deliveries that became widespread in 19th-century hospitals and ignorance of aseptic principles during these interventions, which led to a rise of puerperal infections (Semmelweis, 1861). However, sepsis, malnutrition, and poverty were shown to be surprisingly minor determinants of maternal mortality (Loudon, 2000). In fact, the documented elevated mortality for young adult females in

medieval Sweden implied an even higher maternal mortality than in the 18th and 19th centuries (Högberg *et al.*, 1987).

Many authors also noted a lower life expectancy of young adult females in osteoarchaeological series of all epochs from the Mesolithic up to modern times (e.g. Acsádi & Nemeskéry, 1970; Sayer & Dickinson, 2013; Gilchrist, 2018), although it remains unclear whether other causes such as chronic malnutrition might help explain differences in life expectancy between males and females (Wells, 1975). Less contentious are analyses of 128 pre-Columbian female mummies from northern Chile at the age of reproduction, which indicated a surprisingly high overall maternal mortality of around 14% (Arriaza, Allison & Gerszten, 1988). The earliest direct indications of birth-related mortality come from fetal skeletons found within the mothers' pelvis; the oldest three date to between 37 and 10 ka (Nava *et al.*, 2017), suggesting that maternal mortality was not uncommon in the Upper Palaeolithic. In addition, Vallois (1937) inferred a high prevalence of childbirth-associated deaths in Neanderthals based on the observation that all individuals older than 40 years in the sample were males, and thus that females aged 20 to 40 likely had a higher mortality rate compared to males. However, larger sample sizes are needed to support this conclusion.

These mortality rates are surprisingly similar to those of current hunter–gatherer populations. For instance, a study on the Hiwi from Venezuela estimated a birth-related maternal death rate of about 4.4 per 1000 reproductive-aged women per year (Hill, Hurtado & Walker, 2007), which translates to a maternal death rate of 1300–1800 per 100000 live births (based on a 3–4 year birth interval). In the Aché of eastern Paraguay, a maternal death rate of 1 per 150 births was reported (667 per 100000; Hill & Hurtado, 1996). Higher maternal mortality rates are reported for the Agta of the Philippines and the Hadza in Tanzania with 3520 and 1022, respectively, per 100000 live births, which is greater than the already

alarmingly high Tanzanian national average of 770 per 100000 births at that time (Early & Headland, 1998; Blurton Jones, 2016). This high incidence of maternal morbidity and mortality in traditional, and particularly hunter–gatherer societies supports the notion that human birth is risky even in non-medicalised settings. Moreover, it allows for speculation that even before the adoption of agriculture during the Neolithic transition childbirth was associated with an elevated risk of morbidity and mortality.

Maternal mortality may result from a multitude of factors, and their relative significance may have changed throughout different temporal, geographic and cultural contexts. Nevertheless, one of the most important factors is obstructed labour, which is defined as the failure of the fetus to progress through the birth canal despite strong uterine contractions. Obstructed labour is estimated to be directly responsible for 8–17% of all maternal deaths, and for up to 30% of maternal morbidity in developing countries, second only to excessive blood loss and puerperal infection (Royston & Armstrong, 1990; Prual *et al.*, 2000; Dolea & Abouzahr, 2003). This corresponds to an incidence of between 1.5% and over 17% of all births worldwide, depending not only on the geographical region but also on the definition used (Dumont *et al.*, 2001; Dolea & Abouzahr, 2003; Say *et al.*, 2014). Today, obstructed labour remains among the most common medical indications for a Caesarean section and instrument-assisted delivery (Villar *et al.*, 2006). Its indirect toll may be underestimated as deaths that happen because of obstructed labour and its sequelae are difficult to assess. Moreover, many causes of haemorrhage and childbed fever are causally linked to obstructed labour and the long-term damage of the maternal pelvic organs through prolonged pressure of the fetal head during the first stage of labour (Royston & Armstrong, 1990). In addition to mortality, potentially life-threatening morbidities associated with obstructed labour include perineal tears, uterine infection and rupture, pelvic organ prolapse and obstetric fistulae, which can also carry significant stigma and potential social exclusion (Schneider, Husslein & Schneider, 2016; Bashah *et al.*, 2019).

Obstructed labour also poses serious risks for neonates, such as oxygen deprivation and related brain damage and perinatal death, but also infection and brachial plexus lesions (Dammann & Leviton, 2000; Jorch & Hübner, 2010). Whereas neonatal infection may have other causes than obstructed labour, intrapartum-related hypoxic events are, with 8.5 cases per 1000 live births, a leading cause of neonatal mortality and morbidity, contributing to the death of 2 million babies and over 400000 impaired survivors globally each year (Lawn *et al.*, 2009; Lee *et al.*, 2013).

The leading cause of obstructed labour is a mismatch between fetal head size and the dimensions of the mother's pelvis. Termed cephalopelvic disproportion, this mismatch is particularly relevant to understanding how the risks of childbirth relate to the 'fetopelvic' fit. Cephalopelvic disproportion accounts for about 65% of obstructed labour instances, the remainder being mostly attributed to malpresentation and malposition (Gessessew & Mesfin, 2003). Cephalopelvic disproportion becomes more frequent with

larger neonates (>4000 g) (Boulet *et al.*, 2003; Zhang *et al.*, 2008), although a large neonatal head is more strongly associated with complicated labour than is high birth weight (Elvander, Hökberg & Ekéus, 2012; Lipschuetz *et al.*, 2015). Another serious, although rarer, complication of high birth weight (>4500 g) is shoulder dystocia, arising when the mother's pubic bones obstruct the fetus' shoulders (Nesbitt, Gilbert & Herrchen, 1998; Trevathan & Rosenberg, 2000).

Birthing positions may play an important role in mediating the incidence of obstructed labour and birth progress. Compared to the supine, semi-recumbent lithotomy position that has become the norm in hospital settings of many countries, semi-upright postures like squatting and kneeling allow gravity to facilitate the descent of the fetus and significantly increase pelvic diameters in the midplane and outlet (Reitter *et al.*, 2014; Hemmerich, Bandrowska & Dumas, 2019). Upright maternal positions, e.g. squatting, were argued to have a slight advantage over supine positions in terms of the duration of the second stage of labour and by reducing the frequency of assisted deliveries (Priddis *et al.*, 2012; Gupta *et al.*, 2017), although two systematic reviews failed to find a statistically significant difference (Gupta *et al.*, 2017; Dokmak *et al.*, 2020). There was also no clear difference in terms of Caesarean section rates (Gupta *et al.*, 2017) or the risk was found to be higher in squatting positions (Dokmak *et al.*, 2020). On the other hand, upright positions were associated with an increased risk of blood loss and possibly perineal tearing (Gupta *et al.*, 2017; but see Dokmak *et al.*, 2020). These findings call into question whether the increases in pelvic dimensions documented in imaging studies of upright positions actually translate into a meaningful reduction in birth difficulty (Gupta *et al.*, 2017; Dokmak *et al.*, 2020).

In any case, inefficient birthing positions do not explain the high prevalence of maternal morbidity and mortality in hunter–gatherer populations, nor in past European societies, where semi-erect postures seem to have been standard until the transition from home births to birthing in hospital settings in the late 19th century (Gupta & Nikodem, 2000). Presently, 63% of global deliveries still take place at home, mostly in rural areas of developing countries (Bang *et al.*, 2004), where non-supine positions often predominate. Yet, a study from India shows that nearly 15% of women who give birth at rural homes potentially need emergency obstetric care (Bang *et al.*, 2004).

Human childbirth therefore remains fundamentally associated with mortality and morbidity, which raises the question of how a process that is imperative for survival and reproduction could be so risky, and which selective pressures are ultimately responsible for maintaining such a precarious birth process.

(2) The 'Obstetrical Dilemma'

Humans are not only unusual among primates in their large brain size at birth, but also in having neonates that are twice as big as those of great apes (Leutenegger, 1982; Martin, 1983; Wells *et al.*, 2012). Either a more capacious birth canal, requiring a larger pelvis, or a smaller newborn

would theoretically ease the cephalopelvic fit and reduce the risk of obstructed labour. Yet, birth weight and neonatal brain size are both strongly positively associated with infant survival rate up to a certain optimum (Karn & Penrose, 1951; Alberman, 1991; Zhang *et al.*, 2008), and brain size has clearly been the target of directional selection in our lineage. Contrary to the expectation that our pelvis may have co-evolved with the increase in brain (and thus head) size, the human pelvic canal seems to have become markedly shorter anteroposteriorly, as well as slightly narrower mediolaterally as compared to great apes (Table 1), possibly resulting in the complex birth process typical for human females. This apparent paradox has implicated opposing selective pressures related to the evolution of bipedalism and rapid encephalisation that resulted in an ‘obstetrical dilemma’ in our lineage (Fig. 1; Washburn, 1960).

The notion of the obstetrical dilemma itself has a complex history, in part because its constituent ideas seem to have been around in some form since the early 20th century. One harbinger was Gregory (1928), who was the first to describe trade-offs arising from the evolution of an upright posture and bipedal locomotion in humans. Krogman (1951) elaborated on this by referring to these features as ‘scars of human evolution’. Specifically, he described adaptations to bipedalism, including an evolutionary shortening of the ilium and lowering of the sacrum following divergence from the last common ancestor with great apes. Krogman identified these pelvic changes, in combination with our bigger heads, as the source of increased birth difficulties in modern humans. From the fetal perspective, Lane (1903) suggested that maternal pelvis size determines fetal size at term and thus its growth rate, which was supported by Thoms & Godfried (1939). Further, Portmann (1941), based on Bolk’s (1926) neoteny theory, discussed the immaturity of human newborns and pointed out that the degree of neurological and physical development, as well as the slowdown in overall growth velocity of a one-year-old human baby, paralleled those of a newborn chimpanzee. However, owing to its simplicity, Portmann (1941) was sceptical of the idea that the size of the maternal pelvis alone could be a limiting factor of fetal head size.

It was not until 1960 that Sherwood Washburn formally combined these ideas in a popular science article focused on brain evolution and tool use, where the term ‘obstetrical dilemma’ made its formal debut. Stimulated by the accumulating evidence of early hominin fossils and associated stone tool assemblages, Washburn pointed out that although the ischium of *Australopithecus* was still long, ilium length became reduced during the early phase of human evolution as an adaptation to bipedal locomotion, which shortened the distance between the sacroiliac and hip joints, thus decreasing the size of the birth canal (Fig. 2; Washburn, 1960, 1963). Since brain size (and newborn body size) also increased during human evolution, the resulting ‘dilemma’ was arguably solved by delivery of the fetus at an earlier stage of development, rendering it effectively helpless. The term ‘obstetrical dilemma’, however, did not immediately gain traction among the scientific community; in fact, Trinkaus (1984) referred to the same phenomenon as a ‘reproductive dilemma’. It was Rosenberg (1992) who eventually introduced it to the anthropological literature, adding pelvic sexual dimorphism as a second solution to the dilemma. It is well known that modern human females and males on average have a markedly different pelvic shape. Schultz (1949) and Leutenegger (1970, 1982) described similar differences, specifically in relative pubic length, in non-human primates with comparably large neonatal heads. Since the pubic bones contribute to pelvic canal size, and thus to obstetric sufficiency, they attributed this dimorphism to differential selection in males and females.

An important modification to the original obstetrical dilemma concept occurred when the focus shifted to pelvic width (breadth). Krogman (1951) and Washburn (1960) had pointed to the anteroposterior narrowing of the birth canal that coincided with the onset of habitual bipedalism in the earliest hominins (see also Kummer, 1965, 1975). Later this was reframed to the notion of increased locomotor efficiency deriving from decreased pelvic width (Rosenberg, 1992), which built upon the pelvic remains available in the hominin fossil record. The pelvis of *Australopithecus* was reconstructed with an exceptionally wide mediolateral breadth (Lovejoy, Heiple & Burstein, 1973; Lovejoy, 1979; Tague & Lovejoy, 1986; but see Häusler & Schmid, 1995,

Table 1. Female human pelvic dimensions expressed as ratios to the same dimensions in apes (*Hylobates*, lar gibbons; *Gorilla*, gorillas; *Pongo*, orangutans; *Pan*, chimpanzees). AP, anteroposterior (or sagittal); ML, mediolateral (or transverse); Bi-acetab., bi-acetabular breadth. Pelvic depth refers to the craniocaudal length of the pelvic canal. All dimensions are body size-corrected using femoral head diameter

Comparison (normalised to femoral head diameter)	Inlet AP ^a	Inlet ML ^a	Midplane AP ^a	Midplane ML ^a	Bi-acetab. ^b	Sacrum ML ^a	Pelvic depth ^a
<i>Homo: Pan</i>	0.61	0.93	0.85	0.88	0.86	1.35	0.52
<i>Homo: Gorilla</i>	0.64	0.97	0.90	0.96	0.92	1.36	0.57
<i>Homo: Pongo</i>	0.56	0.84	0.80	0.90	0.81	1.19	0.55
<i>Homo: Hylobates</i>	0.56	0.83	0.79	0.78	0.82	1.07	0.50

^aData from Tague (2005).

^bData from Ward *et al.* (2018) for apes and DelPrete (2019) for humans.

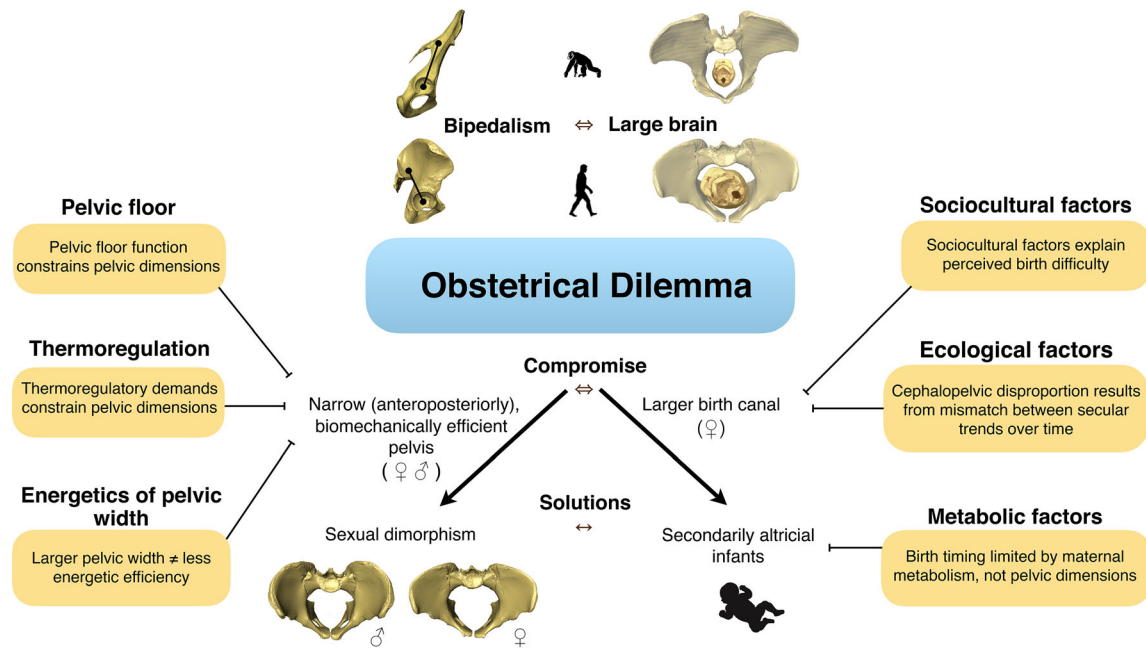


Fig 1. Schematic showing the original obstetrical dilemma hypothesis and complementary or alternative explanations (orange lozenges) as they relate to specific components of the obstetrical dilemma proposed by Washburn (1960). Note that most studies on the pelvic floor, thermoregulation, and energetics to date have focused on pelvic width rather than on the anteroposterior pelvic shortening emphasised by Washburn (1960).

1997), in contrast to modern humans, a feature that was interpreted to be relevant for locomotion but obstetrically superfluous (Rak, 1991). Similarly, Neanderthals were found

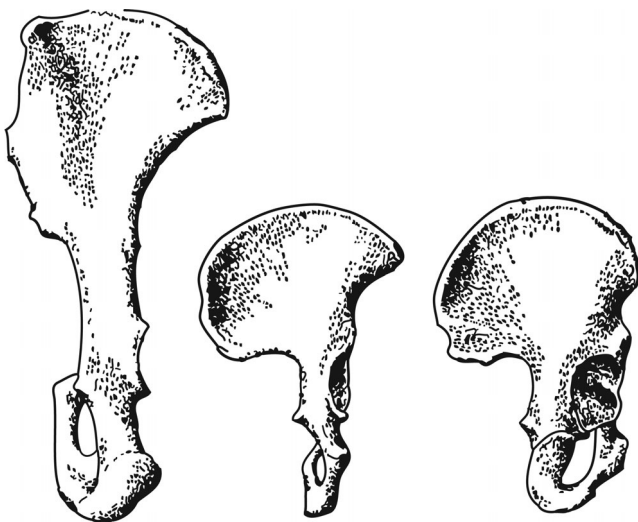


Fig 2. The hipbones of a chimpanzee (left), *Australopithecus* (centre) and a modern human (right) according to Washburn (1960). In his work on the obstetrical dilemma, Washburn used this illustration to emphasize the shortening of the ilium during the evolution of bipedalism. The corresponding anteroposterior shortening of the birth canal, rather than the transverse narrowing that is commonly mentioned, led him to propose the obstetrical dilemma concept.

to have a remarkably long pubis, which was initially interpreted to imply a broader pelvis and longer gestation duration compared to modern humans (Trinkaus, 1984; but see Rak & Arensburg, 1987).

In the last decade or so, the obstetrical dilemma, both as a *hypothesis* (or a collection of hypotheses) as formulated by e.g. Washburn (1960) and Rosenberg (1992), and as the *phenomenon* of an evolutionary trade-off owing to antagonistic selection pressures acting on the human pelvis, has been the target of many discussions and critiques. However, such studies are often only able to address specific aspects of the obstetrical dilemma given its multifactorial nature. As such, many have focused on particulars like compiling evidence for functional trade-offs in pelvic breadth (e.g. Gruss & Schmitt, 2015; Warrenner *et al.*, 2015; Gruss, Gruss & Schmitt, 2017; Wall-Scheffler & Myers, 2017; Whitcome, Miller & Burns, 2017; Grunstra *et al.*, 2019; Pavličev, Romero & Mitteroecker, 2019), evaluating secondary altriciality in humans (Dunsworth *et al.*, 2012; Dunsworth, 2016), discussing how an already challenging evolutionary situation is exacerbated by behavioural and environmental changes (Wells *et al.*, 2012; Wells, 2015, 2017), investigating the role of thermoregulation (e.g. Ruff, 1991, 1994; Gruss & Schmitt, 2015), or emphasising biocultural considerations (Stone, 2016). Most of these aspects are complementary to explaining the complex phenomenon of difficult birth in humans (Fig. 1). By contrast, a few researchers have made efforts to evaluate critically multiple facets of the obstetrical dilemma hypothesis through empirical testing (Dunsworth *et al.*, 2012) or on theoretical grounds (see Dunsworth, 2016, 2018), subsequently advocating rejection of the hypothesis in

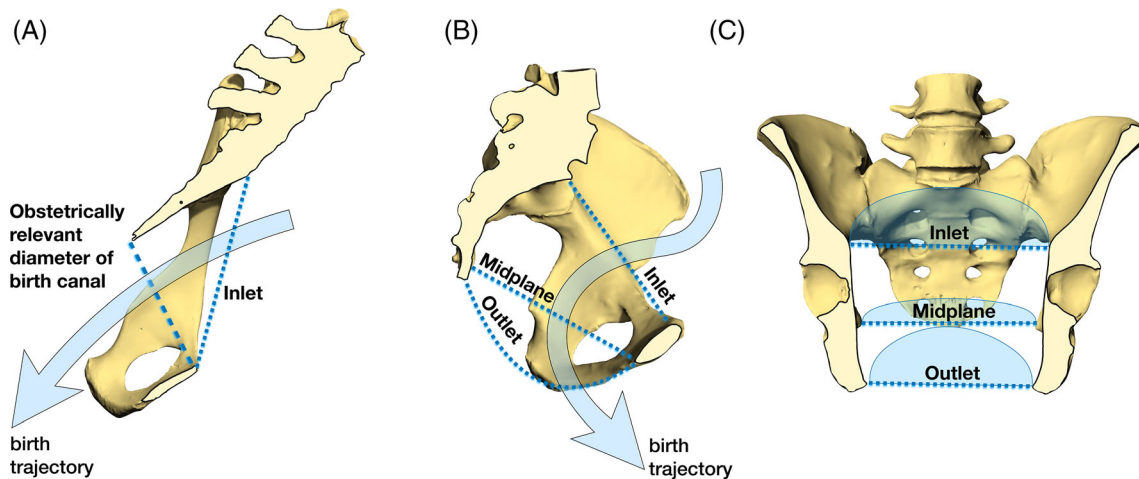


Fig 3. Sections through the bony birth canal. (A) Chimpanzee in lateral view. The bony portion of the birth canal is an almost straight, short tube with the pelvic inlet being an oblique plane to its longitudinal axis; only the anteroposterior diameter perpendicular to the longitudinal axis is obstetrically relevant. (B, C) Modern human in lateral and in anterior view, respectively. The birth passage is curved and begins at the pelvic inlet, is mediolaterally narrowest at the midplane between the ischial spines and widens again at the outlet between the ischial tuberosities.

its entirety (e.g. Dunsworth, 2016, 2018; Nowell & Kurki, 2020).

One objective of this review is to explore the validity and utility of the ideas that shaped the original obstetrical dilemma in the mid-20th century, and those that have since developed from them. In an effort to advance the debate, we also identify important outstanding questions and directions for future research that may elucidate the origins of the complex human birth process.

II. THE BIRTH PROCESS

To determine whether human birth is uniquely difficult, it is necessary to compare the human birth process to that of our zoological relatives, the non-human primates. Despite being broadly similar, human birth differs from that of other primates in several ways that warrant evolutionary explanations.

Firstly, due to our anteroposteriorly shortened and convoluted pelvic anatomy and large fetal dimensions, human birth typically involves a complex and specific sequence of head rotation, flexion and restitution, along with shoulder rotation that aligns the fetus with the convoluted shape of the human bony birth canal to allow successful passage (Figs 3, 4) (Rosenberg, 1992; Abitbol, 1996; Rosenberg & Trevathan, 2002; Trevathan, 2015). Dorsally, the fetus navigates a trajectory that follows the lumbar and sacral curvatures and the inward-protruding coccyx, or tailbone (Schneider *et al.*, 2016). In non-human primates, the birth canal is shorter and shaped more like an oblique ring than a tube. This bony ring is generally sagittally (dorsoventrally) elongated, permitting the fetus

to maintain its orientation as it descends along a relatively straight path.

Additionally, contrasting with other primate species, obstructed labour is more common in humans. Although direct observational data from the wild remain sparse, birth seems to progress comparatively easily for most non-human primates (Lindburg, 1982; Turner *et al.*, 2010; Nguyen *et al.*, 2017). Nevertheless, instances of obstructed labour have been reported for both diminutive marmosets and small-bodied squirrel monkeys (*Saimiri sciureus*) (Abee, 1989; Debyser, 1995) as well as medium-sized macaques (*Macaca mulatta* and *M. fascicularis*) and baboons (*Papio* spp.) (Schultz, 1949; Schlabritz-Loutsevitch *et al.*, 2018). A study on a large sample of captive pigtailed macaques (*Macaca nemestrina*) reported a surprisingly high incidence of difficult births at 14%, while in some captive squirrel monkey populations the occurrence may be as high as 50% (Bowden, Winter & Ploog, 1967; Stockinger *et al.*, 2011). Since these species give birth to neonates with relatively large head sizes compared to the mother's pelvic dimensions – similar to the ratio observed for humans (Schultz, 1949; Leutenegger, 1970) – it is often assumed that birthing difficulties in macaques and squirrel monkeys are the result of cephalopelvic constraints. Yet, in a captive colony of pigtailed macaques, most birth difficulties turned out to be due to malpresentation, particularly breech positions (Stockinger *et al.*, 2011). Breech presentations were also found to be a major cause (25%) of dystocic births in baboons (Schlabritz-Loutsevitch *et al.*, 2018), and they seem to explain most birth difficulties in squirrel monkeys and other non-human primates (Bowden *et al.*, 1967; Stoller, 1995).

In humans the neonatal head is large relative to the maternal pelvic canal, which is represented by a higher cephalopelvic ratio than in most other primates. High cephalopelvic ratios have also been reported for some smaller monkeys

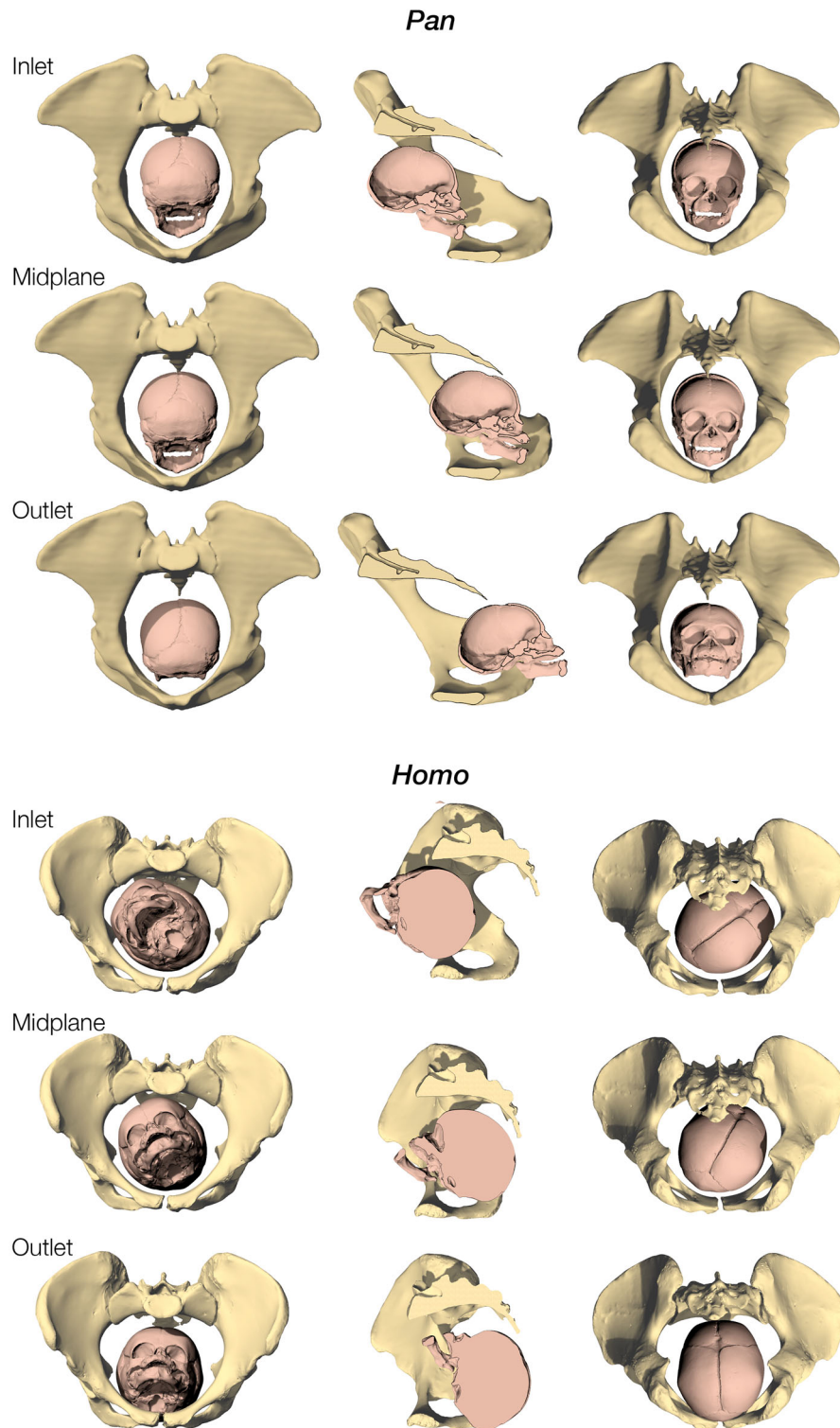


Fig 4. Comparison of the birth mechanism in chimpanzees (top) and modern humans (bottom), in superior view, longitudinal section, and inferior view at the pelvic inlet, midplane and outlet. In chimpanzees, the fetal head is likely extended throughout the birth process, i.e. in a mentum anterior orientation as it usually occurs in non-human primates, but the fetus can also be born with a flexed head as in humans. In humans, the fetal head is flexed and its orientation adapts to the changing shape of the different pelvic planes.

Cephalopelvic proportions:

Different adaptations hominins and monkeys:

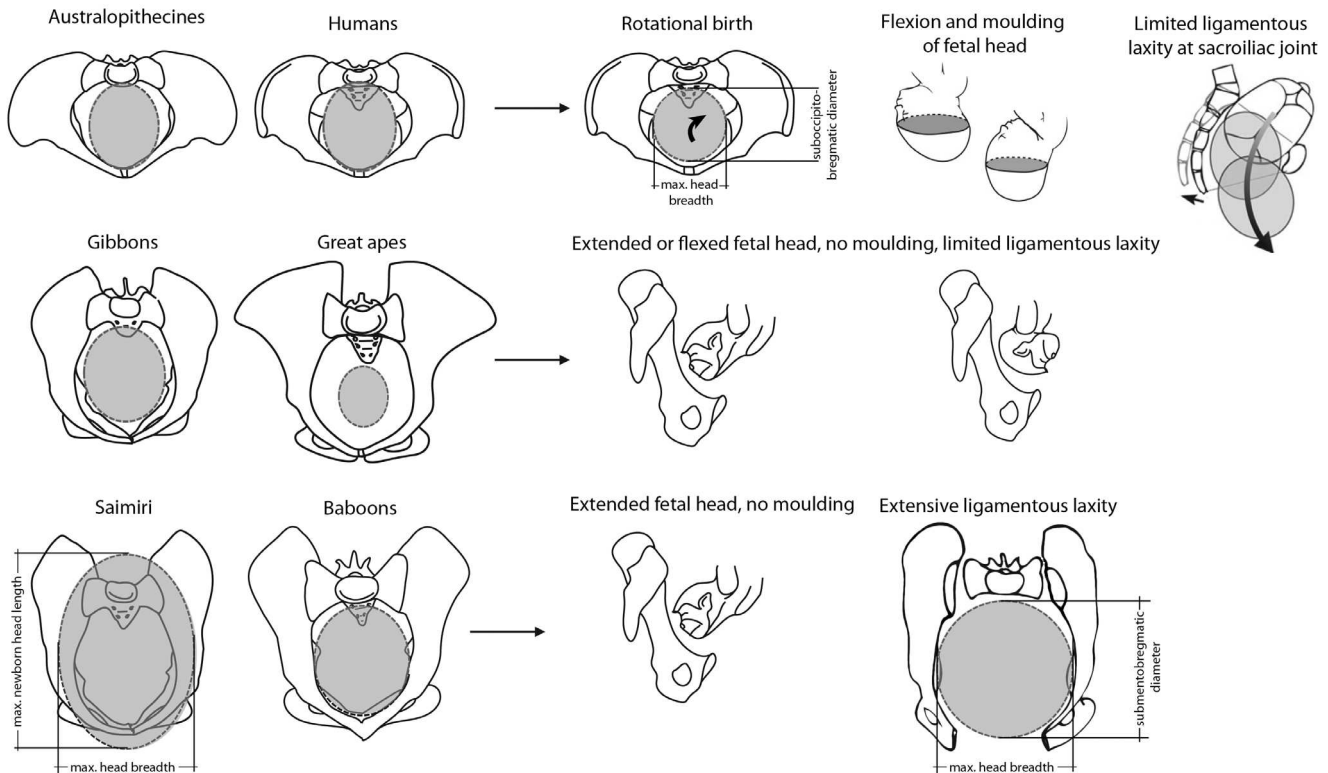


Fig 5. Relationship of the maternal pelvis and fetal head during birth and adaptations to reduce cephalopelvic disproportion. The traditional cephalopelvic proportions according to Schultz (1949) and Leutenegger (1982) are misleading, since maximum length and breadth of the fetal head in relation to the dimensions of the mother's pelvic inlet (left, superior view) are of little obstetrical relevance. Adaptations to high cephalopelvic proportions in humans (and probably in australopithecines) include an elaborate rotational birth mechanism and fetal neck flexion that reduce the diameter of the fetal head, head moulding afforded by open cranial sutures and fontanels, and sacral nutation up to 2 cm permitted by limited sacroiliac joint laxity. In great apes, the relatively small fetal size does not require pronounced adaptations, resulting in only subtle pelvic sexual dimorphism, and neonates are born with either an extended or flexed neck. In small-bodied monkeys and gibbons, fetus head size might significantly exceed the size of the mother's pelvis, and adaptations to ease birth include pronounced ligamentous laxity particularly at the pubic symphysis and extension of the neck of the fetus so that the smaller submento-bregmatic diameter is presented rather than the maximum length of the head adapted from (Stoller, 1995).

and apes, for instance, squirrel monkeys, macaques, and lar gibbons (*Hylobates lar*) (Schultz, 1949; Leutenegger, 1970; Rosenberg & Trevathan, 2002). However, these values are misleading and likely overestimate the tightness of the cephalopelvic fit because they are based on specific fetal head dimensions and maternal pelvic dimensions that are both obstetrically irrelevant. For example, the monkey fetal neck is typically extended during parturition, resulting in a 'mentum anterior', or face, presentation. As such, the submento-bregmatic height (face length) rather than the longer occipito-frontal diameter of the neonatal head is the obstetrically relevant measure (Fig. 5; Stoller, 1995). Moreover, the obstetrically relevant dimension of the pelvic canal in non-human primates is the shortest diameter that is perpendicular to the birth trajectory, while the anteroposterior dimension of the (obliquely oriented) pelvic inlet is less relevant for birth

(Fig. 3). Conversely, in modern humans the pelvic inlet is usually perpendicular to the birth trajectory and the fetus engages the birth canal with a flexed head, leading to an 'occiput' presentation as sometimes also occurs in great apes. Accordingly, the obstetrically relevant head length is actually the suboccipito-bregmatic diameter, which also is considerably shorter than the greatest head length.

The tight cephalopelvic fit in humans is mitigated by the open fontanelles that render the human neonatal head highly malleable during birth. In non-human primates, this type of cranial moulding is restricted due to the almost closed fontanelles at the time of birth (Schultz, 1969), suggesting reduced cephalopelvic constraints relative to humans (Stoller, 1995). On the other hand, monkeys have a short and straight sacrum and some experience significantly increased relaxin-mediated ligamentous flexibility at the pubic symphysis and

sacroiliac joint (Hisaw, 1926; Hartman & Straus, 1939), which significantly increases pelvic canal area, as documented for both baboons and squirrel monkeys (Stoller, 1995) (Fig. 5). Contrastingly, humans (and probably great apes) experience only a limited degree of mobility *via* the sacroiliac joint, as the distal tip of the sacrum can rotate backwards a maximum of 2 cm (Borell & Fernström, 1957; Ohlsén, 1973). An even smaller increase in flexibility occurs at the human pubic symphysis during late pregnancy (on average 3 mm; Becker, Woodley & Stringer, 2010). This relative inflexibility in the human pelvis may reflect our upright, bipedal mode of locomotion which requires increased stability.

Lastly, in monkeys, the offspring is generally born facing the mother's abdomen, which permits the mother to help guide and remove the infant from the birth canal (Trevathan, 2015). By contrast, the human fetus usually exits facing away from the mother, or in occiput anterior presentation, which has been argued to be an important factor for why humans commonly require assistance during birth (Trevathan, 2015). Interestingly, in chimpanzees (*Pan troglodytes*), our closest living relatives, neonates are born facing either the abdomen or the back of the mother at about equal frequencies (Nissen & Yerkes, 1943; Hirata *et al.*, 2011), possibly because pelvic constraints are notably low due to a smaller neonate-to-pelvic size ratio. Overall, compared to non-human primates, the human birth process seems to be more complex and difficult, primarily due to greater cephalopelvic constraints arising from the relatively inflexible pubic symphysis and the contorted shape of the birth canal.

III. BIRTH TIMING

Washburn (1960, p. 74) proposed that the “delivery of the [human] fetus at a much earlier stage of development” compared to non-human primates was the solution to the obstetrical dilemma. Because Washburn did not specify what was meant by an earlier stage of development, this ambiguity has been misleading and often interpreted as humans having a truncated gestation time. For example, Trinkaus (1984) suggested that gestation length in Neanderthals was significantly longer than in present humans owing to their longer pubis and inferred larger birth canal, leading him to speculate that gestation was shortened in anatomically modern humans as a consequence of their increased locomotor efficiency. The discovery of the first complete Neanderthal pelvis, Kebara 2, has since refuted this claim by demonstrating that pelvic inlet size was not proportionately larger than in modern humans and therefore inferred gestation length was also not different (Rak & Arensburg, 1987).

Human pregnancy is, in fact, on average 2 to 3 weeks longer than in orangutans and gorillas, and 5 to 7 weeks longer than in chimpanzees (Martin, 2007; Barton & Capellini, 2011). Moreover, relative to adult body size, human gestation is close to

the overall average primate condition (Martin, 1990). Only when adult brain size is used to scale gestation length in a comparative context, does humans' high degree of encephalisation lead to a deceptively short relative gestation length (Dunsworth *et al.*, 2012). As such, adult human brain size is exceptionally large, rather than gestation length being unexpectedly short. The fact that human gestation is approximately as long as expected for a primate with our body size has been used as evidence against the obstetrical dilemma hypothesis (e.g. Dunsworth *et al.*, 2012). Similarly, genetic studies looking for evidence of positive selection in human evolution for pre-term birth have yielded inconclusive results (e.g. LaBella *et al.*, 2020).

On the other hand, Portmann (1941) contemplated why gestation in humans is not even longer than in great apes given the helplessness of human babies at birth, their non-adult-like body proportions, and the relationship of longer gestation length with higher ‘organisational complexity’ observed among mammals. Portmann (1941) specifically pointed out that human infants continue to grow in length and body mass at the same rate as *in utero* for about 12 months postpartum, while growth velocity in non-human primates slows down at or near birth. Furthermore, human-specific behaviour, vocalisation, upright posture, locomotor capabilities, and adult-like body proportions develop only gradually and reach a comparable state of development to that of newborn great apes during the first year after birth. Portmann (1941) therefore termed this first year the ‘Frühzeit’, or extrauterine fetal time (sometimes imprecisely translated as ‘extrauterine spring’). Based on this, Portmann (1941) proposed that humans would require a gestational length of about 21 months to attain the same degree of physical, neurological and cognitive development as that found in newborn non-human primates.

Later work also supported a two-phase growth trajectory of human brain size, in which the latter continues to grow at a rapid fetal rate until the growth rate eventually slows down shortly after the end of the first year of life, whereas in macaques, for example, this slowdown occurs already at birth (Gould, 1977; Martin, 1983; Halley, 2017). The proportion of neonatal brain size relative to adult brain size is on average 27–29% in humans and about 40% in chimpanzees (Martin, 1983; DeSilva & Lesnik, 2006). Brain size in humans achieves 40% of adult brain size by about 7 months after birth according to Dunsworth *et al.* (2012), and these authors therefore suggested that the extrauterine fetal time of humans is only seven rather than 12 months. Nevertheless, humans take distinctly longer than great apes to achieve the same state of neurological development. Moreover, Portmann (1941) characterised human neonatal immaturity in terms of several aspects of sensory-motor and physical development, not only based on differences in newborn-to-adult brain size proportions, which he argued are not very different in hominoids. In fact, DeSilva & Lesnik (2008) suggested that, when compared to seven other catarrhine species, human neonates have exactly the brain size expected given our adult brain size (but see Martin, 1983).

Despite the large human body size at birth and a gestation length that is not shorter than expected for our body size, the greater prematurity of the human brain at birth and the resulting helplessness of human infants nevertheless contrasts with the considerably more developed, precocial non-human primates, a condition termed ‘secondary altriciality’ by Portmann (1941). Altricial neonates are proposed to be the ancestral state among placental mammals (Portmann, 1939; Martin, 2007), and in this particular instance, the term ‘secondary’ refers to the reversion to an ancestral condition that was lost in primates and then regained as a derived condition in humans. The applicability of the label ‘secondary altriciality’ to humans has been questioned by Duns-
worth (2016, 2018) on the grounds that we are not born after a short gestation period at a very premature stage of development (e.g. when eyes and ears are still closed), as is typical for the altricial offspring of most rodents and carnivores. But the evolution of complex traits is generally not reversed to the exact ancestral condition (Gould, 1970), and neither altriciality nor precociality are discrete, monolithic packages of traits. They may therefore change in different ways depending on the phylogenetic lineage. In this sense, human newborns are the most altricial among primates based on their relatively underdeveloped motor and sensory abilities. However, Schultz (1969) demonstrated that the degree and rate of postnatal development among primates lie on a continuum, such that the slow postnatal maturation of humans cannot be called ‘unique’. For example, bush babies and macaques begin to walk within several hours and days, respectively, while chimpanzees and gorillas only do so after about 20 weeks, and humans after about 40 weeks (Schultz, 1969; see also Garwicz, Christensson & Psouni, 2009).

IV. SEXUAL DIMORPHISM

Pelvic sexual dimorphism is another way in which selection can act to minimise anatomical constraints on the birth process. The pronounced degree of pelvic sexual dimorphism in humans in itself offers strong evidence for the notion that the pelvis is subject to conflicting selection pressures, an important consideration for evaluating the existence of an evolutionary trade-off.

Compared to males, human females usually possess a wider sciatic notch, an increased bi-ischial breadth, a longer pubis, a larger subpubic angle, as well as a relatively wider sacrum. All of these features contribute to a more spacious birth canal (Fig. 6). In fact, several dimensions (e.g. sagittal and transverse diameters of the pelvic inlet, midplane, and outlet) of the female pelvis are absolutely as well as relatively larger than in the male pelvis, despite women having a smaller average body size than men (e.g. Tague, 2005; DelPrete, 2019). This high degree of sexual dimorphism is not known elsewhere in the human skeleton, nor is it likely present in the pelvis of most extant non-human mammals

(Tague, 2016). Indeed, various studies have shown that body size differences cannot account for the existence of more birth-amenable size and shape features in the female pelvis of humans and various non-human primates (Gingerich, 1972; Tague, 1991; Arsuaga & Carretero, 1994; St. Clair, 2007; Fischer & Mitteroecker, 2017; Moffett, 2017). Accordingly, human and non-human primate pelvic sexual dimorphism has long been attributed to sex-specific selection associated with parturition in females (Schultz, 1949; Leutenegger, 1974; Tague, 1991; Rosenberg, 1992; St. Clair, 2007; Fischer & Mitteroecker, 2017).

However, recent work has cast doubt on whether the human pelvis is as evolutionarily constrained as a scenario of opposing selection pressures would imply. Adaptive interpretations of sexual dimorphism, specifically in the human pelvis, have recently been criticised on the grounds of differential hormone levels in the sexes being capable of inducing dimorphism in the skeleton (Duns-
worth, 2020). Furthermore, observations of considerable variability in the shape of the female pelvis (Arsuaga & Carretero, 1994; Betti *et al.*, 2013; Kurki, 2013b; Kurki & Decrausaz, 2016), geographical diversity in pelvic form and pelvic sexual dimorphism consistent with neutral evolution (Betti *et al.*, 2013; Betti, 2014; Betti & Manica, 2018), remodelling of female pelvic shape during adulthood (Huseynov *et al.*, 2016), and the role of phenotypic plasticity (Wells *et al.*, 2012) may all indicate a limited role of selection in shaping present sex differences in human pelvic morphology.

From a quantitative genetic perspective, sexual dimorphism originates with opposing, sex-specific selection regimes. Complex sets of quantitative traits, such as pelvic dimensions, are polygenic and many of the genes underlying their development are shared between the sexes (Kenney-Hunt *et al.*, 2008), i.e. the between-sex genetic correlation is high (Lande, 1980). Quantitative genetic work has demonstrated that selection for such a set of traits in one sex will elicit a correlated evolutionary response in the other due to genetic pleiotropy and linkage effects (Lande, 1980). Directional selection in one sex, therefore, does not suffice to bring about sexual dimorphism; it needs to be counteracted by an opposite selection pressure in the other sex, i.e. divergent selection between the sexes, or else the latter sex will simply show a correlated response to selection on the former and no relevant sexual dimorphism will arise (Lande, 1980; Lande & Arnold, 1985). The genes underlying skeletal development are mostly not sex-linked, so if sexual dimorphism in somatic growth is adaptive, sex-specific selection will act on developmental regulatory mechanisms, such as sex-biased expression of shared genes and hormonal modifiers (e.g. sex steroids and their receptors), to achieve sex-specific growth and consequently sexually dimorphic traits (Bernstein & Crelin, 1967; Badyaev, 2002; Parsch & Ellegren, 2013).

However, developmental pathways leading to sex-related skeletal differences in mammals are conserved and include differential sex hormone (e.g. oestrogen, androgen) levels produced by the adrenal and reproductive (gonadal) glands (Lange, Hartel & Meyer, 2003). Sex differences in somatic

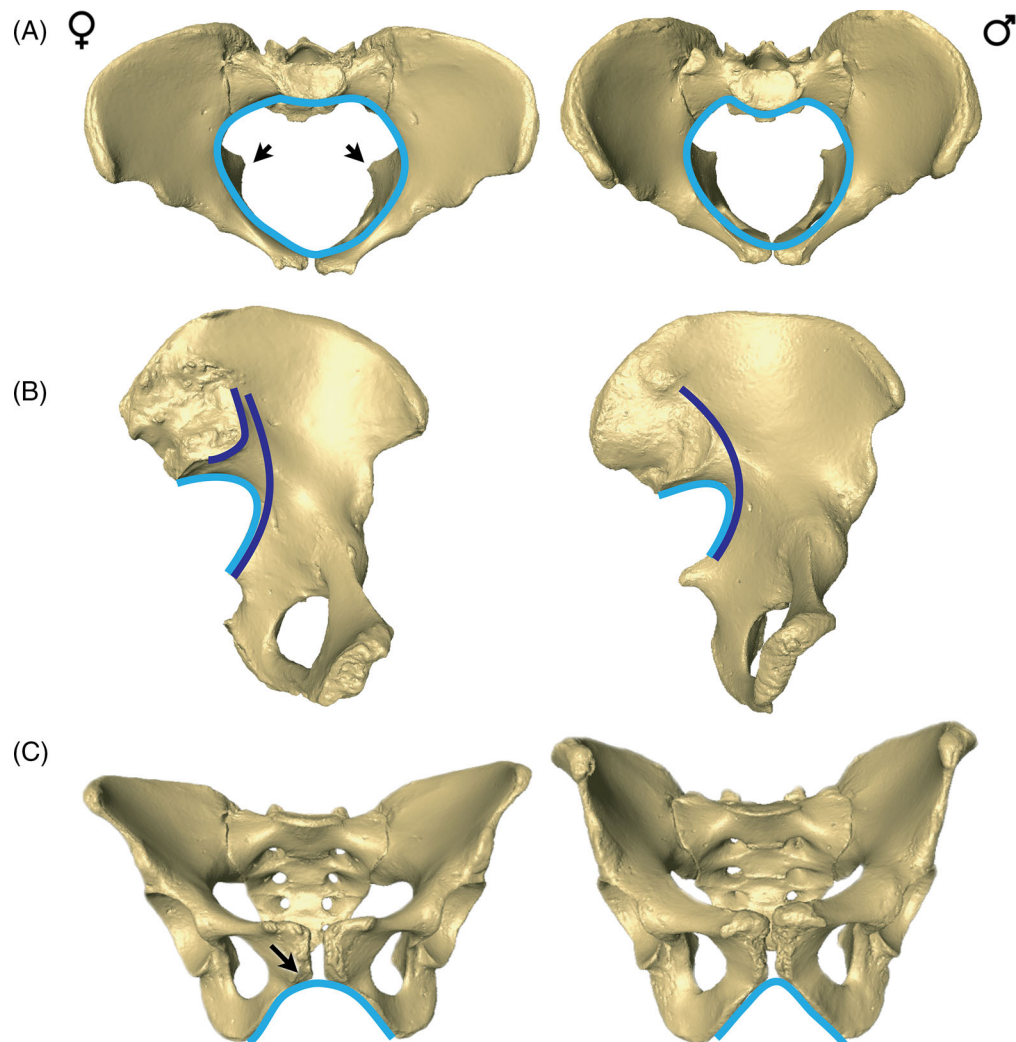


Fig 6. Sexually dimorphic traits typically observed in the human pelvis. (A) The pelvic inlet is often rounder in females and more heart-shaped in males, while the distance between the ischial spines is larger in females (arrows). (B) The greater sciatic notch (light blue) tends to be wider in females and forms a double arch (dark blue) with the auricular surface while males have a narrower greater sciatic notch and no double arch. (C) Females have a wide subpubic angle and ventral arc at the pubic symphysis (arrow) while males usually have a narrower subpubic angle and lack a ventral arc (see Ferembach *et al.*, 1980; Bruzek, 2002).

growth (e.g. stature or pelvic morphology) might therefore be a developmental by-product of selection for sex-differentiated reproductive morphology or other traits with shared underlying biology and are not necessarily the target of direct selection (Dunsworth, 2020). This may explain the apparent ubiquity of some degree of pelvic sexual dimorphism among mammals (e.g. Tague, 2005, 2016; Schutz, Donovan & Hayes, 2009a; Schutz *et al.*, 2009b; Kaufmann *et al.*, 2013; Grunstra *et al.*, 2019). However, the degree and timing of hormone release is only one side of the coin; having sufficient and appropriate hormone receptors is also necessary to enable target cells to bind and respond to hormone signalling (Beato & Klug, 2000). Whereas release of hormones is systemic (i.e. they are released into the bloodstream), the distribution of hormone receptors varies locally (Smith *et al.*, 1990) and between the sexes (Franz, Wendler &

Oetting, 1996), which likely enables hard and soft tissues to develop more or less pronounced differences among the sexes. Indeed, research documenting a decoupling between the degree of sexual dimorphism in skulls *versus* pelvis of the same individuals [humans: Best, Garvin & Cabo (2018); grey foxes (*Urocyon littoralis*): Schutz *et al.* (2009b)] supports this assertion. The spatial pattern of hormone receptivity is thus another potential pathway through which natural, e.g. obstetric, selection can bring about sex differences in hard and soft tissue morphology. In fact, the existence of more pronounced pelvic sex differences in mammals that give birth to relatively large neonates as well as the presence of pelvic dimorphism in species that are monomorphic in body size (e.g. Hisaw, 1924; Tague, 2005, 2016; Moffett, 2017; Grunstra *et al.*, 2019) may be explained by this potential mechanism (Fischer *et al.*, 2021).

Although the developmental and endocrine pathways to sexual dimorphism are evolutionarily conserved, they are not inconsistent with adaptive scenarios. The pattern of sexual dimorphism in the human pelvis is opposite to that in human body size, indicating that pelvic dimorphism is not a simple corollary of the hormone-driven induction of long bone growth. The magnitude of human pelvic sexual dimorphism is marked when compared to the often much subtler dimorphism in non-human mammals, including our phylogenetically closest ape relatives (Tague, 2005; Fischer *et al.*, 2021). It is therefore unlikely that sex differences in the human pelvis can be explained by the action of sex hormones alone; rather, they are more likely the result of a combination of existing developmental machinery and direct, antagonistic selective forces (Fischer *et al.*, 2021).

A more spacious pelvic canal is favoured by obstetric selection in females to accommodate the birth of a large offspring. This is supported by the observation that non-human primates with high cephalopelvic indices and large neonates show stronger pelvic sexual dimorphism, which includes size and shape features resembling those in humans (Gingerich, 1972; Leutenegger, 1974; Moffett, 2017; Zollhofer, Scherrer & Ponce de León, 2017). The presence of obstetric selection is further suggested by the adaptive covariance between stature, head size, and pelvic inlet shape in humans, whereby women with a larger head and women of shorter stature (both of which may increase the risk of obstructed labour; Dujardin, VanCutsem & Lambrechts, 1996) tend to have rounder pelvic inlets, which might ease childbirth (Caldwell & Moloy, 1938; Stewart, Cowan & Philpott, 1979), compared to smaller-headed and taller women (Fischer & Mitteroecker, 2015). Similar patterns of covariance between pelvic shape and fetal head were recently also discovered in rhesus macaques (*Macaca mulatta*), and were observed to ameliorate the tight fetopelvic fit that characterises these monkeys (Kawada *et al.*, 2020).

Selection favouring a small pelvis, on the other hand, may act on men and women alike (e.g. because of bipedalism, Washburn, 1960) or on men alone (e.g. for male reproductive functionality; Pavličev *et al.*, 2019).

However, the universal pattern of sexual dimorphism in the human pelvis (Betti & Manica, 2018; DelPrete, 2019) does not mean that other, non-selective factors, such as plasticity and population history do not influence human pelvic morphology, or discount the possibility that women navigate obstetric or locomotor selection in different ways, resulting in subtle population differences.

V. ALTERNATIVE AND COMPLEMENTARY VIEWS TO THE OBSTETRICAL DILEMMA HYPOTHESIS

(1) Variability of pelvic shape

A key implication of the obstetrical dilemma hypothesis is that, because birth-related selection acts on women only,

human males and females are subject to partly different selection regimes, yielding anatomical differences between the sexes in pelvic shape. In particular, following an initial stage of directional selection, obstetric selection may act as a stabilising force on human female pelvic shape to guarantee passage of the fetus through the birth canal. Accordingly, it has been proposed that stabilising obstetric selection acts to limit phenotypic variability in human female pelvic canal form, specifically size and shape, compared to that in males as well as compared to other skeletal structures (Meindl *et al.*, 1985; Tague, 1989, 1995; DelPrete, 2019).

On the other hand, age has been identified as an additional source of human pelvic variation (Berger *et al.*, 2011), with wider pelvic dimensions associated with prime reproductive age in females and slightly narrower pelvic dimensions in older females (Huseynov *et al.*, 2016; Mitteroecker & Fischer, 2016; Auerbach *et al.*, 2018). These findings evidence continued skeletal remodelling in females throughout adulthood that is observed to a lesser degree among males, a difference likely afforded *via* hormonal regulation (Mitteroecker & Fischer, 2016). This further complicates comparisons of phenotypic variability between the sexes and reiterates the need for studies that adequately account for these changes, as well as population differences.

The developmental trajectory described by Huseynov *et al.* (2016) is likely to increase variability of women in studies examining the 'adult' pelvis without distinguishing between prime reproductive, late reproductive and post-reproductive age groups. This confounding factor may explain the failure of previous investigations to find that human pelvic shape is consistently less variable in females compared to males (Tague, 1989) and other anthropoids (Tague, 1995). The same applies to the finding that pelvic dimensions are not less variable than limb form in either females or males, consequently interpreted as a lack of evidence for the presence of stabilising selection acting on female pelvic canal morphology (Kurki, 2013b). Moreover, much of the variation in pelvic dimensions observed *among populations* of modern humans has been argued to be explicable by neutral evolution (Betti, Cramon-Taubadel & Lycett, 2012; Betti *et al.*, 2013; Betti & Manica, 2018).

Studies focusing on body form and ecogeographic variation confirm the problematic nature of attempting to decipher traits under selection that are constrained by covariation and exhibit considerable variability. This makes it difficult to estimate accurately both the direction and magnitude of selective pressures (Savell, Auerbach & Roseman, 2016). However, there is a lesser degree of morphological integration between the hipbone and the pelvic canal in humans compared to great apes, which means that these pelvic structures are comparatively less developmentally and evolutionarily constrained by each other. This not only increases the evolvability of the human pelvic canal but may also explain the greater-than-expected variability of the human pelvis (Grabowski, Polk & Roseman, 2011; Grabowski, 2013). In addition, the reduced degree of integration between obstetrically relevant (pelvic canal) and less relevant (hipbone) components may itself be

evidence of the pelvis' response to opposing selection regimes and hence confirm the existence of an evolutionary 'dilemma'.

Analysis of the data of Betti & Manica (2018) showed that the anteroposterior diameter of the birth canal in all planes is consistently less variable than its mediolateral diameter across 24 populations. This suggests that these anteroposterior dimensions are under stronger stabilising selection across space and time than their mediolateral counterparts (Table 2). This is consistent with the predictions of the obstetrical dilemma as originally formulated by Washburn (1960).

(2) Energetics of bipedalism

An essential component of the original obstetrical dilemma hypothesis is the notion that bipedal locomotor performance is enhanced by a narrower pelvis, which contributes to a tight cephalopelvic fit (see discussion in Leutenegger, 1974). Originally, the focus was on the phylogenetic reduction in the distance between the sacroiliac and the hip joints in humans and its biomechanical implications for adaptation to an upright posture and sagittal balance of the body (Fig. 2; Krogman, 1951; Kummer, 1959, 1975; Washburn, 1960, 1963). Later publications, on the other hand, were inspired by the fact that – in traditional two-dimensional free-body diagrams of single-legged stance – pelvic width, particularly bi-acetabular breadth, influences energetic efficiency by altering the mechanical advantage of the hip abductor muscles (Inman, 1947; Lovejoy *et al.*, 1973; Ruff, 1995). Over time, this notion of a biomechanically efficient, mediolaterally narrow pelvis has become one of the central tenets of the obstetrical dilemma hypothesis (e.g. Rosenberg, 1992; Dunsworth *et al.*, 2012; Wells *et al.*, 2012; Dunsworth, 2016).

Two alternative predictions flow from the obstetrical dilemma hypothesis: (i) pelvic sex differences are associated with differences in locomotor efficiency, economy, or performance, as observed in locomotion-related pelvic traits; (ii) small or negligible pelvic sex differences exist in locomotion-related pelvic traits and concomitantly, small or negligible differences in locomotor performance are observed between the sexes. The first is the assumption that is most commonly considered and tested (e.g. Dunsworth *et al.*, 2012; Warrener *et al.*, 2015), whereas the second prediction follows from the notion that directional (followed by stabilising) natural selection can limit phenotypic expression to a small range of phenotypes, all of which consequently have a similar functional performance. This makes it difficult to detect correlations between remaining pelvic variation and locomotor performance, especially amidst a plethora of other

factors that affect either pelvic morphology (e.g. ancestry) or locomotion (e.g. age, muscular performance).

Warrener *et al.* (2015), employing both a static and a dynamic biomechanical model, found that the slightly greater pelvic width in women is not associated with significantly increased energetic costs during bipedal walking compared to men (see also Dunsworth *et al.*, 2012; Warrener, 2017). Specifically, their work on hip abductor mechanics revealed that mediolateral ground force production and segmental accelerations associated with the foot and limb influence force production by the abductors so that pelvic width alone offers little predictive power in terms of energy expenditure (Dunsworth *et al.*, 2012). As such, the authors concluded that the obstetrical dilemma hypothesis does not garner sufficient empirical support, given that narrower pelvic dimensions did not appear energetically more efficient.

However, when the data of Warrener *et al.* (2015) are used to fit regression lines to the female and male samples *separately*, a wider distance between the hip joints does appear to be associated with higher locomotor costs in females, but not in males or in the combined sample (Fig. 7). Admittedly, the data are too limited to yield reliable regression lines, but this observation does invite speculation about how increased sample sizes might elucidate a subtle relationship between individual pelvic dimensions and overall locomotor economy. It would furthermore be informative to conduct such work in more diverse samples that vary in geography and age, among others, to represent a broader range of human phenotypes. Ideally, such studies should also test how individual pelvic configurations fare directly in childbirth, which would contribute to our recognition of which features carry implications for childbirth, which influence locomotor performance, and which affect both but with opposite outcomes, i.e. those that contribute to a trade-off.

The work of Warrener *et al.* (2015) demonstrates that the cost of bipedal locomotion is surprisingly similar between the sexes, which may be explained by the extensive overlap in their bi-acetabular width. This overlap suggests that bi-acetabular width could be constrained despite strong sexual dimorphism elsewhere in the pelvis, a finding recovered in other studies as well (e.g. Fischer & Mitteroecker, 2015; DelPrete, 2019). This observation would support, rather than contradict, an evolutionary dilemma, as selection seems to have successfully constrained biomechanically relevant dimensions of pelvic width between the sexes, which may be at, or near, the optimal compromise solution.

Table 2. Variation of human pelvic dimensions across the means of 24 populations, showing that anteroposterior (AP) dimensions are consistently less variable than mediolateral (ML) dimensions (data from Betti & Manica, 2018)

	Inlet ML (cm)	Inlet AP (cm)	Midplane ML (cm)	Midplane AP (cm)	Outlet ML (cm)	Outlet AP (cm)
Mean	12.51	10.70	9.98	12.35	11.95	11.81
SD	0.73	0.44	0.60	0.44	0.80	0.45

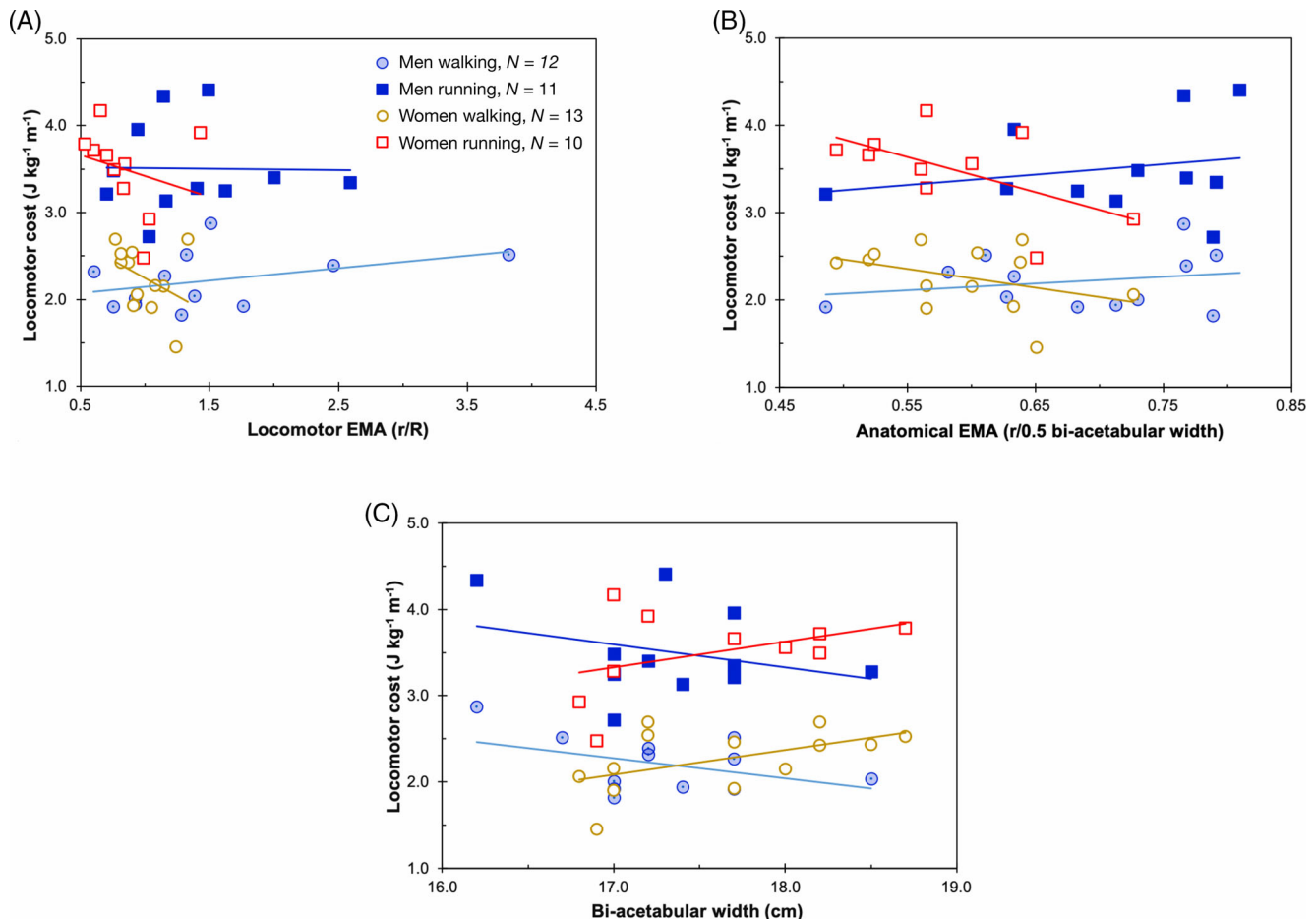


Fig 7. A reanalysis of the data of Warrener *et al.* (2015) demonstrates that locomotor costs of running and walking increase in women but not in men with increasing pelvic width. Least-squares regression lines are calculated for the male and female samples separately. (A) Locomotor costs *versus* hip abductor effective mechanical advantage (EMA) measured dynamically, defined as r/R where r is the abductor muscle moment arm and R is the moment arm of the ground reaction force vector. Lower values of EMA correspond to larger bi-acetabular widths. (B) Locomotor costs *versus* hip abductor EMA measured anatomically. Lower values of EMA correspond to larger bi-acetabular widths. (C) Locomotor costs *versus* bi-acetabular width. Note that the sample size is too small to draw reliable statistical conclusions.

Ruff (2017) suggested that a rejection of the obstetrical dilemma hypothesis based on pelvic width is premature before other important mechanical consequences beyond overall locomotor costs are considered, including how the pelvis and femoral morphology function together as a complex to enable biomechanical efficiency.

Explanations for how pelvic dimorphism could counter disparities in energetic efficiency between males and females have been frequently proposed. For instance, some authors argue that anatomical disparities can be mitigated by kinematic distinctions between male and female walking styles (Whitcome *et al.*, 2017). Based on Rak's (1991) study on the A.L. 288-1 *Australopithecus afarensis* pelvis, Gruss *et al.* (2017) speculated about a potential adaptive advantage of a wider pelvis for short-statured women. Specifically, they found that women with wider bi-trochanteric breadth relative to leg length had slightly longer stride lengths afforded by increased axial rotation of the pelvis. The relatively longer stride

lengths in these individuals required less hip extension and flexion, thereby reducing the vertical displacement of the body's centre of mass and lowering energetic costs. Additional studies corroborate the observation that the increased degree of hip rotation in women increases stride length and thereby decreases the amount of required steps to reach a particular distance, thus improving overall locomotor economy (e.g. Wall-Scheffler & Myers, 2013; Whitcome *et al.*, 2017). Therefore, a mediolaterally wide pelvis in shorter individuals does not necessarily result in a quantifiable negative effect on the overall efficiency of a bipedal gait.

The conclusions of Gruss *et al.* (2017) do not mean that antagonistic pressures related to obstetrics and bipedalism (or some other selective force) are absent from the pelvis. None of this work precludes the aforementioned possibility that the human female pelvis is confined to a particular bi-acetabular width range that is optimally adapted for

bipedalism, outside of which disadvantages exist, and inside of which variation in width has only small effects on locomotor efficiency that are compensated by other anatomical features or changes to gait kinematics (Wall-Scheffler & Myers, 2017).

An alternative possibility is that the pelvis may have evolved to meet other biomechanical requirements, including those necessary to mitigate high joint reaction forces or excessive mediolateral bending that incur potential injury risk and their own energetic costs (Ruff, 2017). In addition, increased stability and speed flexibility over varied terrain, or improved efficiency while carrying certain loads, have been linked to the larger mediolateral pelvic breadth typical of females [see review by Wall-Scheffler & Myers (2017) and references therein]. Hence, even if the pelvis does not contribute to substantial overall differences in locomotor costs between males and females, this does not directly contradict the original idea that bipedalism may favour certain pelvic dimensions.

There may be various other ways in which current human pelvic form is constrained by an upright, bipedal mode of locomotion that simultaneously impose a constraint on birth, but which remain untested. Studies of the biomechanical consequences of variation in anteroposterior pelvic canal length are particularly lacking.

(3) Energetics of gestation and growth

One proposed solution to the original obstetrical dilemma is to give birth to a relatively immature neonate while head size is still small compared to the dimensions of the maternal pelvis, thus implicating maternal pelvic dimensions as the ultimate factor for birth timing. One mechanism involved in the timing of human parturition was identified in the 1980s. Work in sheep led to the discovery of an endocrine ‘clock’ based on the fetal hypothalamic–pituitary–adrenal (HPA) axis that is responsible for a surge of corticotropin-releasing hormone (CRH), and thus cortisol, at the time of birth (Petraglia *et al.*, 1987). Because cortisol is a catabolic hormone involved in the mobilisation of fat reserves, Ellison (2001, 2008) proposed that birth occurs when the energy demands of the fetus exceed the mother’s metabolic capacity to supply sufficient nutrition *via* the placenta. According to this ‘metabolic crossover hypothesis’, labour would thereby start when the fetus effectively begins to starve. This idea was based on the assumption that fatty acids are not able to cross the placenta efficiently. Ellison (2001, 2008) therefore proposed that towards the end of pregnancy the mother may no longer be able to supply the fetus with enough fatty acids to sustain rapid brain growth and to acquire the fat reserves necessary to survive the neonatal period. Since then, experimental and modelling approaches have shown that placental fatty acid transport occurs rapidly and that this process does not seem to represent a bottleneck in terms of the availability of nutrients to the fetus (Haggarty, 2010; Perazzolo *et al.*, 2017; Lewis, Childs & Calder, 2018). This is supported by the observation

that maternal metabolism can supply macrosomic fetuses (weighing up to 10 kg in exceptional cases) with sufficient nutrients, without long-term negative outcomes (Khambalia *et al.*, 2017). Future work is, however, needed to measure the efficiency of fatty acid transfer through the placenta with greater precision and to understand how lipids cross the hydrophilic villous stroma and the endothelium (Lewis *et al.*, 2018).

Dunsworth *et al.* (2012) built upon Ellison’s (2001, 2008) metabolic crossover hypothesis to explain secondary altriciality in humans and the timing of birth. This expanded concept was named the ‘Energetics of Gestation and Growth’ (EGG) hypothesis, which has been argued to be an alternative to the obstetrical dilemma hypothesis by Dunsworth *et al.* (2012) and Dunsworth (2016, 2018). The EGG hypothesis postulates that gestation length is determined by a metabolic constraint that limits maternal energetic investment in the developing fetus. As such, maternal pelvic size has adapted to neonatal head size, not *vice versa*. The neurological immaturity of human newborns is accordingly interpreted as a by-product of a delicate balance between maternal and fetal metabolism bound by a threshold reached when fetal demands exceed maternal metabolic capacity (Dunsworth *et al.*, 2012).

Under the EGG hypothesis, the energy requirement of the fetus is argued to continue to increase exponentially towards the end of pregnancy – based on extrapolation of fetal growth beyond gestational week 36 – crossing the mother’s metabolic ceiling at the time of birth (Dunsworth *et al.*, 2012; see Fig. 8A). However, an alternative interpretation is that a linear rather than an exponential extrapolation of the growth rate is also plausible. Inclusion of the data point two weeks after birth [omitted by Dunsworth *et al.* (2012) in their Fig. 3] shows a decline of the offspring’s energy requirement between gestation week 36 and shortly after birth, which might correspond to the ‘starving phase’ postulated by Ellison (2001, 2008) (Fig. 8B). Thereafter, the same (linear) growth rate as prior to gestation week 36 is resumed before it slows down again 1.5 months after birth and exceeds the mother’s presumed metabolic ceiling at 2.0–2.1 times the basal metabolic rate (BMR) (Fig. 8A) only about 6 months after birth, when the infant is commonly weaned in present-day industrialized societies. This would suggest there is no crossing of fetal and maternal energy requirements at the time of birth.

Dunsworth *et al.* (2012) inferred an upper limit on sustained maternal metabolic scope around $2.1 \times \text{BMR}$, which is just above the metabolic peak observed at the end of pregnancy near $2.0 \times \text{BMR}$ (corresponding to 628 kcal above the energy requirements of a non-pregnant, non-lactating woman). This suggests that women approach a physiological metabolic cap for investment in fetal growth at the end of the third trimester. However, it is well established that, as a result of lactation costs, a mother’s energy investment in her offspring actually increases to a higher level after birth (Butte & King, 2005). Lactation is considered by many researchers to be the most energetically expensive

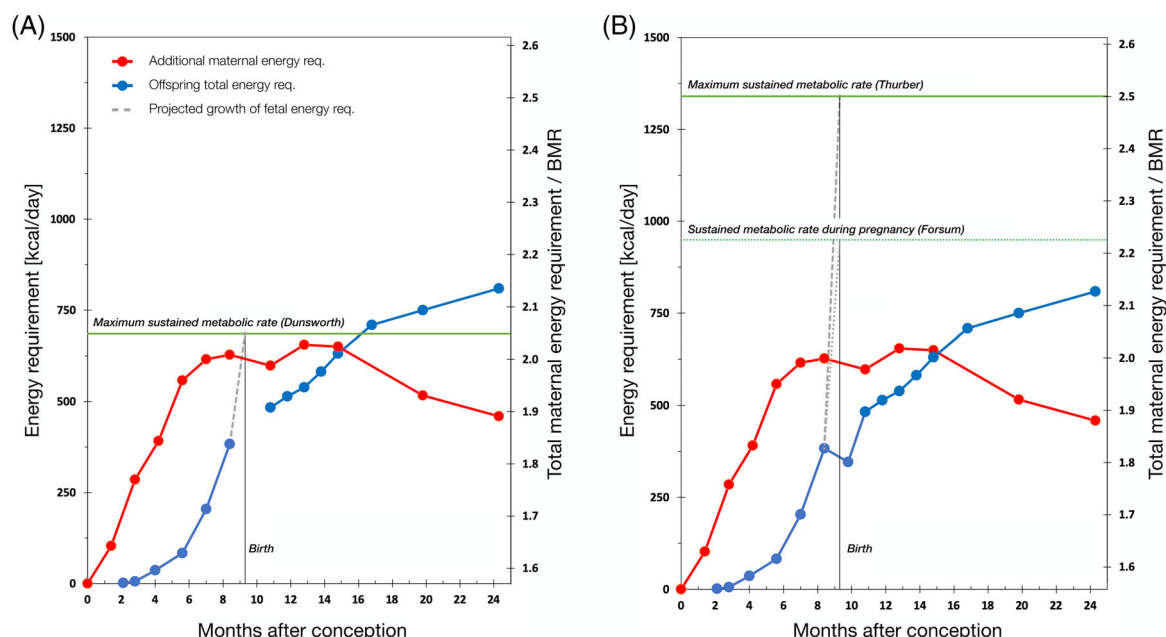


Fig 8. Energy requirement of the offspring compared to the additional energy requirement of the mother during pregnancy and lactation. (A) Maternal energy expenditure (red) approaches a presumed metabolic ceiling between 2.0 and $2.1 \times$ basal metabolic rate (BMR) in the third trimester, while the energy requirements of the fetus increase exponentially towards the end of gestation with a projected crossing of the metabolic threshold of the mother at parturition [data from Dunsworth *et al.* (2012), Table S2]. (B) Alternatively, a higher metabolic ceiling at $2.23 \times$ BMR [as deduced from pregnant women under the 'Forsum, 1992' entry in Table 6 of Butte (2005)] or $2.5 \times$ BMR (as extrapolated from endurance athletic events; Thurber *et al.*, 2019), would suggest that women do not approach their maximum sustained metabolic scope during the third trimester and that fetal growth rate is extrapolated with an extraordinarily steep curve to cross the maternal metabolic threshold at the time of birth. Inclusion of the data point 2 weeks after birth instead shows that, after an initial decline in the offspring's energy requirement, the same (linear) growth rate as prior to gestation week 36 is resumed before it slows down again 1.5 months after birth. The offspring energy demands before and after birth are meant to be directly comparable; they are based on the relationship of total energy expenditure (TEE) to mass in the fetus and on TEE with an allowance for growth in infants (for further details see Dunsworth *et al.*, 2012).

reproductive state in mammals, with various primate species complying with this trend (Sadleir, 1969; Prentice & Prentice, 1988). Humans are no exception, expending an amount of energy in the first 4 months after birth that is equivalent to the total energetic cost of pregnancy itself (Picciano, 2003). Further, the production of breast milk after birth is even more energetically taxing compared to the energy supplied directly to the infant *via* placental transfer (Prentice & Prentice, 1988).

Recently, Thurber *et al.* (2019) suggested that pregnancy might be comparable to ultralong athletic endurance activities, and that for events lasting longer than 140 days the maximum sustained metabolic scope plateaus somewhere around $2.5 \times$ BMR. This would theoretically permit the total energy expenditure required during pregnancy to be more than doubled before a metabolic cap imposed by nutritional absorption limitations is reached. It also implies that women do not necessarily approach a metabolic limit during the third trimester and that they could potentially invest more energy in the fetus. Moreover, if the maximum sustained metabolic scope is closer to $2.5 \times$ BMR rather than $2.1 \times$ BMR, the extrapolated growth rate of the fetus would

need to be extraordinarily steep to cross the maternal metabolic cap at the time of birth (Fig. 8B).

Correlation does not imply causation, and so – although all studies on energy expenditure during pregnancy show that maternal energy turnover peaks around the time of birth (Savard *et al.*, 2021) – it is possible that maternal metabolism has adapted to the duration of gestation rather than *vice versa*. The fact that most women in energetically non-stressed populations gain weight and continue to increase adipose tissue storage particularly during late pregnancy contradicts the notion that maternal energy resources are fully depleted near the time of birth. That there is still much to learn about the energetics of pregnancy is further demonstrated by the fact that some women in the third trimester of pregnancy are able to engage in rigorous endurance exercise, including training for and running marathons competitively. In fact, rigorous physical activity was even found to decrease the risk of prematurity and slightly increase gestational length (Holt & Holden, 2018; Beetham *et al.*, 2019). There are also compensatory mechanisms that modify energy allocation in times of metabolic stress (see Dufour & Sauter, 2002). Evidence from rural populations in Gambia suggest the cost of

pregnancy varies according to the available energy supply, revealing metabolic adaptations for energy sparing that typically manifest as a depression of BMR and the mobilisation of fat reserves to mitigate reduced dietary intake (Poppitt *et al.*, 1993).

Although growing a fetus is indisputably costly in metabolic terms, the maternal pelvis also unquestionably constrains neonatal size and its successful passage during birth in humans (Trevathan & Rosenberg, 2016). This is evidenced not only by the very tight fit between the fetus and the maternal pelvis and the high incidence of cephalopelvic disproportion, but also by the occurrence of birth-related mortality and morbidity among mothers and neonates that is probably far more prevalent than in any non-human primate. Whereas the EGG hypothesis considers the maternal pelvis to have co-evolved with, and adjusted to, maternal metabolic investment during pregnancy, it is also possible that limits to maternal metabolic capacity may have co-evolved with, and adapted to, the mechanical constraints imposed by pelvic form.

During recent years it has become increasingly clear that the timing of human parturition is more complex than a simple endocrine clock involving the fetal HPA axis. This HPA idea served as the basis for the metabolic crossover and EGG hypotheses. In fact, among the animals studied, only sheep appear to rely on the HPA axis as the sole mechanism triggering birth (Menon *et al.*, 2016). By contrast, humans are argued to have developed a coordinated, redundant signal cascade that encompasses multiple 'clocks' with interdependent mechanisms to trigger birth. Variation in individual clock dominance could then also explain the wide range of gestation length observed in humans. These mechanisms include clocks triggered by telomeres and fetal membrane senescence, as well as by inflammatory and mechanical factors, in addition to the endocrine pathway, and metabolic signals are therefore not the only triggers of birth (for a review see Menon *et al.*, 2016).

Regarding mechanical triggers, it has been speculated that a feedback mechanism may exist between the maternal and fetal systems that monitors uterine distension and the amount of space available in the pelvic cavity relative to the fetus growing inside it (Wells *et al.*, 2012; Menon *et al.*, 2016). For instance, strong distension of the uterine wall and fetal membranes has been shown to induce the production of pro-inflammatory cytokines, among other signals, through the process of mechanotransduction, with a threshold value of inflammation now known to be an important parturition trigger (Menon *et al.*, 2016). Furthermore, human birth weight has low heritability, in contrast to early fetal and postnatal weight, implying heightened plasticity of fetal size at term, enabling an adaptive response of the fetus to non-genetic factors (Wells, 2015, 2017). In fact, one study found evidence that maternal pelvic dimensions had reasonably good predictive power for neonatal size, independent of maternal stature, performing even better than maternal body mass index (BMI) (Wells, 2017).

The EGG hypothesis thus offers a valuable perspective on the obstetrical dilemma debate by providing a testable hypothesis related to birth timing. And while it is hard to imagine that metabolic resources are not relevant to understanding human fetal growth and gestation, the EGG hypothesis and the obstetrical dilemma hypothesis do not seem to be mutually exclusive (Shipman, 2013). In order to provide a *full* alternative to the obstetrical dilemma hypothesis, the EGG hypothesis must be able to explain the possible selection pressures that prevent the expansion of the birth canal and induce the evolution of pelvic sexual dimorphism (Trevathan & Rosenberg, 2016), in addition to addressing the high prevalence of obstructed labour typical of modern humans.

(4) Thermoregulation

The need to thermoregulate has long been recognized as a significant selective pressure influencing the evolution of body size and relative body proportions in response to climatic variation in endotherms (Bergmann, 1847; Allen, 1877; Meiri & Dayan, 2003), including humans (Roberts, 1953; Ruff, 1991; Tilkens *et al.*, 2007). The proportional relationship between a body's volume (or body mass) and surface area has direct implications for heat production and conservation, with a smaller or more slender body with relatively longer limbs promoting heat dissipation, and a larger, relatively wider, stockier body with proportionately shorter limbs beneficial for heat retention (Ruff, 1994). Ruff (1991, 1994) expanded on this concept using a cylindrical model for human body shape, demonstrating that surface area relative to volume, or body mass, remains constant as long as torso breadth, proxied by bi-iliac breadth, is also kept constant, despite changes in height. This model forms the conceptual basis for those implicating thermoregulatory demands in the obstetrical dilemma debate (see Gruss & Schmitt, 2015), and it has been used to explain the negative allometry of pelvic breadth relative to stature when tracking hominin body size evolution in the fossil record (Ruff, 1991, 2010).

One consequence of these thermoregulatory constraints is that, within the same climatic zone, pelvic width remains constant regardless of variation in stature. Accordingly, Niskanen *et al.* (2018) observed little temporal variation in bi-iliac breadth over the past 30000 years within Europe despite stature decreasing significantly at the beginning of the Neolithic and increasing again only during the last two centuries. Provided that pelvic shape has remained the same, smaller females are, therefore, predicted to have the same incidence of cephalopelvic disproportions as taller females. In fact, the effect of stature on obstructed labour was found to be relatively weak above approximately the 20th percentile of female body height. As the likelihood of obstructed labour shows an inverse non-linear relationship with maternal stature, only women shorter than about 145 cm to 164 cm depending on the population have increasingly difficult births as measured by Caesarean section frequency

(e.g. Dujardin *et al.*, 1996; Cnattingius, Cnattingius & Notzon, 1998; Brabin, Verhoeff & Brabin, 2002; see also review in Wells, 2017).

Conversely, the association between climatic zones and body shape has been widely documented *across* human populations (reviewed in Betti, 2017). For example, many sub-Saharan populations living in hot climates exhibit an elongated body shape (Ruff, 1994, 2002; Holliday & Falsetti, 1995). Furthermore, bi-iliac breadth has been found to correlate with latitude across a large range, with lower-latitude populations having narrower overall pelvic dimensions (e.g. Kurki, 2013a). Pelvic shape has also been shown to vary with temperature across populations: both relative bi-iliac breadth (Ruff, 2010) and overall pelvic size increase as environments become colder (Betti, 2014). However, because it is a measure of the ‘false pelvis’ that does not contribute to the birth canal, bi-iliac breadth might respond to climatic variation without compromising obstetric sufficiency (Kurki, 2007). The comparatively low integration between different parts of the human pelvis and the associated higher evolvability supports this notion (Grabowski, 2013).

The ability to thermoregulate also interacts with pregnancy: fetal size directly impacts maternal heat production, contributing to heat stress in warmer climates and thus exacerbating the ecological pressures influencing body proportions (Wells *et al.*, 2012). Warmer environments are consequently predicted to exacerbate the obstetrical dilemma by imposing additional antagonistic pressures on the mother’s energetic demands, specifically the need to balance heat production with effective heat loss to avoid thermal stress (see review in Wells *et al.*, 2012).

The inferred constraints on pelvic width imposed by climate also have been suggested to impact obstetrically relevant pelvic dimensions (Ruff, 1994, 2010; Weaver & Hublin, 2009; Kurki, 2013a). Gruss & Schmitt (2015) maintain that the climatic changes that accompanied the emergence of the genus *Homo* and selected for a more elongate and narrower body shape produced an evolutionary conflict in the pelvis that had been absent in the earlier australopithecines (Ruff, 1991) as well as in Neanderthals (Weaver & Hublin, 2009), both of which were reconstructed with wider pelves (*contra* Ponce de León *et al.*, 2008). Gruss & Schmitt (2015) further claimed that the aforementioned evolutionary conflict led to a compensatory expansion in the anteroposterior dimensions of the lower (but not upper) planes of the birth canal in anatomically modern humans, resulting in the complex rotational birth mechanism observed in humans today. However, the alleged increase in temperatures in sub-Saharan Africa during the early Pleistocene contrasts with the general cooling trend and the shift to a more arid climate (deMenocal, 2004). Moreover, the supposed increase in anteroposterior dimensions ignores the fact that anteroposterior and mediolateral dimensions impact the body’s surface-to-volume proportions equally.

Increased frontal loads imposed by pregnancy and child-carrying are expected to have significant effects on the mother’s metabolic costs and choice of locomotor speed,

which may vary between climatic zones given different thermoregulatory constraints on body shape and locomotor costs. Experimental work conducted by Wall-Scheffler & Myers (2013) suggested that women with wider pelves have increased flexibility in optimal walking speed, from which they inferred that high-latitude populations with wider pelves gain both thermoregulatory and locomotor benefits (Wall-Scheffler & Myers, 2013). However, only 5.2% of the variation in optimal speed flexibility could be explained by bi-trochanteric breadth (i.e. pelvic width) alone. Moreover, Wall-Scheffler & Myers (2013) did not find a clear association of pelvic breadth with the minimum cost of transport nor with optimum walking speed; bi-trochanteric breadth only marginally increased stride length ($R^2 = 0.003$) and slightly decreased stride frequency ($R^2 = 0.005$), both weakly benefiting gait kinematics. These data therefore suggest that pelvic width, and by extension thermoregulatory factors, seem to play a minor role in locomotor efficiency between different climatic zones. However, more experimental data, especially from people spanning a larger range of geographical and morphological variation are needed.

As a complex, multifunctional structure, the pelvis is undoubtedly subject to various selection pressures, and the role of thermoregulation in exacerbating the tight fetopelvic fit warrants further study. To our knowledge, no studies exist that have revealed a correlation between obstructed labour and body shape. The high rates of maternal mortality in many sub-Saharan countries are probably explained mostly by socio-economic factors rather than by body shape, which is supported by equally high maternal mortality rates in Europe during previous centuries (see Section I). Even main proponents of the thermoregulatory hypothesis posit that, despite the influence of thermodynamics on pelvic form, it is premature to dismiss the role of bipedalism because other complex biomechanical and obstetric-based constraints may simultaneously influence pelvic dimensions (Ruff, 2017). Additionally, as pointed out by Wells *et al.* (2012), the true impact of thermal load on pelvic dimensions remains poorly understood, especially when considering how these factors change throughout pregnancy and the compensatory capabilities of the mother’s metabolism to avoid thermal stress (e.g. fat reduction, activity adjustment).

(5) Pelvic floor stability

The selective pressure for a narrow pelvic canal, especially regarding the distance between the ischial spines in the mid-plane (Fig. 6A) might also be influenced by the need for a strong and supportive pelvic floor to minimise the risk of pelvic floor disorders (Abitbol, 1988). The human pelvic floor is composed of multiple muscles, ligaments and fasciae (sheets of connective tissue) suspended inside the pelvic canal. This includes the pelvic diaphragm, i.e. the levator ani and its fasciae, which evolved from muscles originally important for tail movement, and the thin urogenital diaphragm (Elftman, 1932; Benninghoff & Drenckhahn, 2008). The main functions of the pelvic

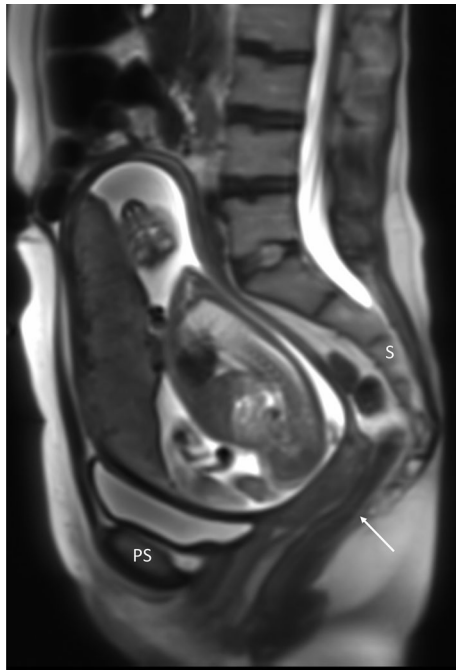


Fig 9. Magnetic resonance image of a pregnant woman, midsagittal plane, (courtesy of Tanja Restin, University of Zurich). Note the oblique orientation of the pelvic floor (arrow) and the position of the pubic symphysis (PS) relative to the fetus and the sacrum (S).

floor are to assist bladder and bowel control and evacuation, help support the pelvic viscera (including a gravid uterus in pregnant women), and contribute to male and female reproductive functioning (Ashton-Miller & DeLancey, 2007; Myers & Smith, 2019).

Whereas earlier publications (e.g. Abitbol, 1988) described the orientation of the human pelvic floor as 'horizontal', it actually has an oblique orientation (Fig. 9). Visceral and fetal weight are thus supported not only by the pelvic floor but also by the pubic bones. Nonetheless, the support function of the pelvic floor is more important in upright humans than in quadrupeds (Elftman, 1932; Abitbol, 1988). It has been proposed that the larger the human pelvic canal, the more displacement is seen in the pelvic floor, other things being equal. Accordingly, a smaller pelvic canal and more pronounced ischial spines arguably enhance its support function (Abitbol, 1988; Brown *et al.*, 2013). The 'pelvic floor hypothesis' thus posits that, in addition to bipedal locomotion, pelvic floor stability is an important factor in constraining pelvic canal shape.

Pelvic floor disorders, including incontinence and pelvic organ prolapse, are frequent among women, and can have detrimental impacts on physical, psychological, and reproductive health (e.g. Wall, 1999; Kenton & Mueller, 2006). Stress urinary incontinence, for example, is well known to be associated with increased abdominal pressure and loading impact from the viscera on the pelvic floor muscles during activities such as jumping, running, sneezing or coughing

(Bø, 2004). Pregnancy and vaginal delivery are well-known risk factors for pelvic floor dysfunction and injuries (e.g. Kearney *et al.*, 2006; Lukacz *et al.*, 2006; de Tayrac & Letouzey, 2016). However, although the risk of pelvic floor disorders increases significantly with age and parity, it is also common among young and nulliparous women (e.g. Hendrix *et al.*, 2002; Lawrence *et al.*, 2008; Nygaard *et al.*, 2008). The pelvic floor hypothesis supposes that the frequency of these disorders is the product of an evolutionary conflict between the capacity to give birth to large babies and having a sufficiently supportive pelvic floor (Grunstra *et al.*, 2019; Pavličev *et al.*, 2019).

Support for the pelvic floor hypothesis comes from medical studies that found positive associations between wider pelvic dimensions and a higher incidence of pelvic floor dysfunction in women, after controlling for confounding factors such as age and parity (Sze *et al.*, 1999; Handa *et al.*, 2003; Stav *et al.*, 2007). However, other studies failed to detect a correlation of bony pelvic canal dimensions with pelvic floor disorders (Stein *et al.*, 2009; Li, Song & Ma, 2015). Such inconclusive findings may result from a weak signal-to-noise ratio in clinical data and the influence of various other factors that contribute to the development of pelvic floor disorders, making it difficult to isolate the effect of bony pelvic form. For example, both a reduced lumbar lordosis (the inward curve of the spine) and an increased thoracic kyphosis (which leads to a compensatory reduction in lumbar lordosis) have been associated with a higher incidence of pelvic organ prolapse, probably because they lead to a less oblique and more horizontal pelvic floor orientation (Lind, Lucente & Kohn, 1996; Nguyen *et al.*, 2000). The development of pelvic floor disorders has also been attributed to the additive effects of the gradual ageing of connective tissues, hormonal changes and even routine strain associated with conditions like constipation (Ashton-Miller & DeLancey, 2007; Lawrence *et al.*, 2008). However, a recent finite element study isolated the effect of pelvis size by holding other parameters (e.g. material tissue properties) constant, and found that larger pelvic floors, as defined by their radial dimensions, show disproportionately large downward deformations compared to smaller pelvic floors. These findings corroborate the hypothesis that a larger bony pelvic canal results in a relatively higher degree of pelvic floor deformation under the same intra-abdominal pressure, which undermines the support function of the pelvic floor and may increase the risk of pelvic floor disorders, such as prolapse (Stansfield *et al.*, 2021).

Grunstra *et al.* (2019) noted strong sexual dimorphism in the pubic symphysis of bats, with females consistently showing a pubic 'gap' while males typically have a fused symphysis. This pubic gap is an obstetric adaptation to birthing large fetuses that comprise 10–45% of maternal weight (Crelin, 1969; Grunstra *et al.*, 2019). But the lack of a closed bony pelvic ring likely also affects where muscles and ligaments of the pelvic floor attach to their bony support and consequently impacts the supportive capacity of the pelvic floor. Grunstra *et al.* (2019) proposed that bats were able to

evolve this highly sexually dimorphic trait because they are flying mammals that mostly roost upside-down, with both features likely to significantly reduce gravitational forces acting on their pelvic floor.

Proponents of the pelvic floor hypothesis have mostly argued for, or assumed, the selective benefits of a strong and supportive pelvic floor regardless of sex (Abitbol, 1988). But others raised the possibility that a narrow pelvis may be favoured especially in human males due to its potential benefits for male reproductive functions – and hence male reproductive fitness – such as sustaining erection and preventing sexual dysfunction (e.g. premature ejaculation) caused by a weak pelvic floor musculature (Grunstra *et al.*, 2019; Pavličev *et al.*, 2019). In a sample of Europeans and South and North Americans, erectile dysfunction affected 16% of men aged 20–75 years with exact numbers varying by country, age category, and degree of severity (Rosen *et al.*, 2004; see also Johannes *et al.*, 2000; Nicolosi *et al.*, 2003). Although the incidence of erectile dysfunction increases strongly with age, 26% of all patients with erectile dysfunction are younger than 40 years (Capogrosso *et al.*, 2013). Pavličev *et al.* (2019) further drew on the observation that pelvic floor exercises can improve erectile dysfunction (Myers & Smith, 2019). Although age and cardiovascular diseases are among the chief known risk factors for erectile dysfunction, this does not rule out a contribution of bony pelvic dimensions *via* pelvic floor strength, even if to a comparatively small degree (Pavličev *et al.*, 2019). A potential connection between weaker pelvic floor muscles and larger bony pelvic dimensions in men with erectile dysfunction has not been tested and requires further study. This male-specific view offers a novel and interesting direction for future research concerning the obstetrical dilemma.

(6) Nutrition and phenotypic plasticity

It has also been argued that the fit between the maternal bony pelvis and the fetus is mediated by environmental factors that affect maternal and fetal growth, and thus that contemporary incidences of cephalopelvic disproportion are not the same as those experienced by earlier members of *Homo sapiens*. This view, predominantly promoted by Wells and colleagues (e.g. Wells *et al.*, 2012; Wells, 2015, 2017; Wells *et al.*, 2018), emphasises that the obstetrical dilemma – defined as the *phenomenon* of tightly fitting maternal pelvic and fetal dimensions – is not evolutionarily fixed, but is subject to non-genetic mechanisms that are environment dependent. Moreover, the one-generation lag between mother and offspring means that ecological conditions may vary between the timing of maternal skeletal growth and subsequent growth of the fetus, further impeding phenotypic integration between pelvic and fetal size (Wells, 2015; Zaffarini & Mitteroecker, 2019). Maternal and fetal growth show high levels of phenotypic, specifically developmental, plasticity in response to nutritional stress and disease load, with some environmental stressors having antagonistic effects on the maternal and fetal contributions to the fetopelvic fit.

The emergence of agriculture, as a case in point, was associated with a shift from a high-protein, low-carbohydrate diet to a low-protein, high-carbohydrate diet. This resulted in a well-documented reduction in adult stature in numerous human populations due to the poorer nutritional quality afforded by the agricultural diet and an increased infectious disease load resulting from sedentary living (see review in Wells *et al.*, 2012; Wells, 2015). It is often assumed that a reduction in stature is accompanied by smaller pelvic dimensions (Abitbol *et al.*, 1997). Indeed, as discussed in Section V.4 for thermoregulation, short maternal stature below a threshold at about the 20th percentile is associated with an increased risk of cephalopelvic disproportion (Dujardin *et al.*, 1996; Sheiner *et al.*, 2005; see also Wells, 2017). At the same time, the high glycaemic load of carbohydrate-rich diets is associated with obesity and increased neonate weight (Clapp, 2002). Gestational diabetes, for which obese and shorter women are at an increased risk, can lead to an abnormally large birth weight [fetal macrosomia (>4000 g); Wells *et al.* (2012) and references therein]. Nutritional stress can thus lead both to stunted growth in childhood and obesity in adulthood, which has been dubbed the ‘dual burden of malnutrition’ (Wells, 2017; Wells, Wibaek & Poullas, 2018). In turn, this nutritional burden can exacerbate the tight fetopelvic fit and has been proposed to explain elevated levels of obstructed labour, Caesarean sections, and infant mortality on the populational level (Wells, 2017; Wells *et al.*, 2018), but also in specific subgroups of various modern human populations, e.g. in Southeast Asian immigrants in the United States (Abitbol *et al.*, 1997) and in under-resourced communities in Mexico (Mendez-Dominguez *et al.*, 2021).

In some cases, poor-quality nutrition not only leads to shorter maternal stature and a potentially narrower pelvis, but it can also lead to reduced fetal growth (e.g. Konje & Ladipo, 2000; Christian, 2010; Özaltın, Hill & Subramanian, 2010). Where undernourished mothers are more likely to have smaller infants, birth difficulty is expected to stay constant as long as the nutritional situation remains unchanged (Abitbol *et al.*, 1997). Nonetheless, current levels of obstructed labour and related birth complications seem to represent, in part, responses to relatively recent ecological changes, which mainly involve secular trends in maternal obesity that are substantially stronger than those in stature. This has therefore been argued to constitute a ‘new obstetrical dilemma’ (Wells, 2017).

Intergenerational improvements in living conditions, rather than the obesity epidemic, have also been invoked to explain the recent surge in rates of obstructed labour and Caesarean sections in many countries (Zaffarini & Mitteroecker, 2019). Despite an initial decrease in stature, coinciding with the transition from a hunter-gatherer lifestyle to a more sedentary, agricultural lifestyle at the beginning of the Neolithic, humans have grown taller on a global level during the last one to two centuries to return to the stature that was typical during the Pleistocene (Niskanen *et al.*, 2018). This increase in body height has been steeper

in some countries than others, sometimes within a single generation. In populations where this is the case, fetuses likely develop in an improved environment compared to their mothers, and because the fetus is one generation ahead of the mother, these swift intergenerational changes in nutritional and health conditions may lead to a fetal size that exceeds the size of the birth canal, causing a population-level increase in rates of obstructed labour (Abitbol *et al.*, 1997; Zaffarini & Mitteroecker, 2019). Indeed, among a number of socio-economic and epidemiological predictors (including obesity), the degree of secular increase in human stature was the best predictor of Caesarean section rate on a global level (Zaffarini & Mitteroecker, 2019).

Other factors may help explain contemporary and past rates of fetopelvic disproportion and obstructed labour through their effect on maternal pelvic growth, such as maternal age, (micro)nutrient deficiency, and disease. A deficiency in certain micronutrients can also curb pelvic growth, notably the lack of calcium and vitamin D. A mild deficiency of vitamin D of less than 37.5 nmol/l was found to be associated with an increased risk of Caesarean sections (Merewood *et al.*, 2009), while severe vitamin D deficiency in children can lead to rickets and in adults to osteomalacia, both with concomitant skeletal and pelvic deformities. The Industrial Revolution saw high levels of malnutrition and low sunlight exposure, which resulted in an epidemic of rickets and osteomalacia. Because the associated pelvic deformities often caused obstructed labour, rickets was the most severe risk factor for maternal death in many parts of Europe until the beginning of the twentieth century (Loudon, 1992; Skippen, 2009).

Ecological and epidemiological approaches thus explicitly address factors that exacerbate an already-challenging evolutionary scenario. They primarily seek to explain the recent surge in the incidence of, and global variability in, obstructed labour rather than explaining the selective forces that have been acting to constrain the widening of the birth canal and which underlie sexual dimorphism in the human pelvis.

VI. OUTLOOK

This review demonstrates that, despite some opposition to specific aspects of the obstetrical dilemma hypothesis, a complete dismissal of its entire theoretical foundation is not justifiable given current data. Many additional explanations surrounding the obstetrical dilemma have been put forth over the decades since Washburn's (1960) publication, which have significantly advanced our understanding of the complexity of causal and contributing factors, how they interrelate and where they might offer complementary or competing explanations.

The fact that natural selection – expected to minimise strongly adverse fitness outcomes – has not managed to eliminate the high levels of mortality and morbidity associated with human birth continues to be a puzzling observation.

Recently, theoretical modelling of the underlying evolutionary trade-off dynamics in the human pelvis have shed light on this paradox. Mitteroecker *et al.* (2016) showed that even weak selection for large-headed newborns and a narrow pelvis, resulting in a tight fetopelvic fit, is sufficient to explain the prevalence of cephalopelvic disproportion observed in human populations and hence the persistence of an obstetrical dilemma.

Further investigations into the different components of the obstetrical dilemma are warranted – notably that birth canal size is constrained by bipedalism specifically, as opposed to other selective agents such as pelvic floor stability, and that birth canal size in turn constrains further intrauterine fetal development. For example, future research initiatives could focus on correlating biomechanical function and performance with pelvic shape *via* more experimental work, focusing not only on dimensions of pelvic breadth but also on anteroposterior depth. Further exploration into the interaction between soft and hard tissues of the pelvis will help to identify additional constraints related to pelvic dimensions. Finally, additional research into the metabolic capacities of pregnant women in different populations, including women partaking in sustained endurance activities and those residing in non-industrialised settings, is needed to advance our understanding of birth timing.

In recent years, an additional perspective introduced to the obstetrical dilemma debate has begun to shape the discourse around human childbirth and must therefore briefly be acknowledged here. It concerns a biocultural perspective that considers birth-related problems as a recent cultural phenomenon heavily influenced by a patriarchal society (Stone, 2016). This view furthermore maintains that, by alleging that birth complications have an evolutionary component, the scientific community is masking bigger issues like the over-medicalisation of childbirth (in some countries) and health care disparities experienced by marginalised groups. This criticism seems to be supported by global statistics, including the disparity in regional Caesarean section rates and the influence of, for instance, poverty on birth outcomes. Bias introduced by the medical industry may impact birth outcomes by providing financial incentives, using supine birth positions despite evidence that other postures could facilitate easier births, and having obstetricians rather than midwives assist at birth (see review in Dunsworth, 2016). Specifically, doctor bias, related to both experience level and the desire to preserve leisure time, have been found to influence the decision to perform Caesarean sections (e.g. Costa-Ramón *et al.*, 2018). The emphasis of such cultural aspects has enabled more rigorous exploration of factors confounding the obstetrical dilemma debate, and more importantly, has highlighted systemic bias in medical practice. Nonetheless, high maternal and neonatal mortality and morbidity is also characteristic of non-medicalised and hunter-gatherer societies. Accordingly, a productive balance must be struck between an adequate understanding of the risks of birth and the prevention of its unnecessary over-medicalisation. Therefore, while seeking to empower women when it comes

to natural birth, we must acknowledge that some require assistance due to biological, potentially evolutionarily derived, circumstances beyond their control.

A further aspect to consider is the inconsistent use of the term ‘obstetrical dilemma’ in the literature. This term was coined by Washburn (1960) to propose constraints on pelvic shape due to opposing selection pressures from bipedalism and encephalisation, solved by the evolution of ‘secondary altriciality’ in humans. Rosenberg (1992) expanded the hypothesis by including sexual dimorphism as a second solution to the obstetrical dilemma, and adapted the hypothesis further, maintaining that the selection pressure acts on mediolateral width of the pelvis rather than its anteroposterior diameter. Other scholars use the term ‘obstetrical dilemma’ to refer to the notion of an evolutionary trade-off between obstetrics and any opposing factor, whether or not it is bipedalism. Further, some refer to the tight fetopelvic fit without explicitly addressing an evolutionary trade-off. Imprecise usage of the term ‘obstetrical dilemma’ generates confusion and conflation of different ideas. For the sake of clarity in the debate, we recommend that usage of the term ‘obstetrical dilemma’ be confined to the original ideas as phrased by Washburn (1960) with Rosenberg’s (1992) expansion to include sexual dimorphism. Deviating concepts should be identified and named individually to avoid propagating confusion.

VII. CONCLUSIONS

- (1) Human birth is complex and risky when compared to non-human primates owing to the convoluted shape of our pelvis and the tight feto-pelvic fit. This is reflected by the curved, multi-rotational trajectory of the fetus through the maternal pelvis and the globally high incidence of obstructed labour that results from this close fit. By contrast, difficult birth in non-human primates is mainly due to malpresentation, while their cephalopelvic fits are relaxed by a markedly higher degree of ligamentous flexibility of the symphysis and sacroiliac joints compared to humans.
- (2) The human pelvis constitutes an evolutionary compromise between opposing selection pressures favouring a spacious birth canal in women as well as a smaller, mainly anteroposteriorly shorter, but (to a lesser degree) also a mediolaterally narrower pelvis in both sexes compared to non-human primates. Empirical support for the existence of an evolutionary trade-off resulting from antagonistic selection regimes comes from the pronounced degree of human pelvic sexual dimorphism, the tight fit between fetal and maternal pelvic dimensions, and the covariance between female head size and female pelvic shape, which collectively reduce the likelihood of a cephalopelvic mismatch.
- (3) The obstetrical dilemma hypothesis *sensu* Washburn (1960) and Rosenberg (1992), whereby bipedalism is

proposed to limit pelvic dimensions, cannot be rejected based on current data. More experimental work is required to elucidate differences in energetic efficiency of bipedal walking and running in association with variation in other pelvic dimensions, and particularly in terms of anteroposterior (sagittal) dimensions. This could provide a new direction for future testing and is expected to advance research on this topic.

- (4) The suggestion that women closely approach a metabolic ceiling in late pregnancy, and that this determines birth timing, has not been explicitly tested. Ongoing research on both physiological constraints and genetic processes implicated in the initiation of birth are important avenues to evaluate the EGG hypothesis and its assumptions. As such, further investigation is needed to test where the metabolic cap in pregnant women actually lies, which compensatory mechanisms can be used to avoid reaching it, and whether it theoretically could be crossed by the fetus at the time of birth. However, even if a metabolic threshold dictates the timing of birth, it does not disprove obstetrical and biomechanical constraints on the pelvis, as these can exist simultaneously.
- (5) Various hypotheses have been proposed to explain the tight fetopelvic fit and associated birth complications in humans, and several of these, notably those pertaining to pelvic floor stability, thermoregulation, and phenotypic plasticity are not mutually exclusive or incompatible with the obstetrical dilemma hypothesis. Most pertain to different levels of explanation, i.e. they explain a certain part of the variation in pelvic shape of modern humans, or they address individual components (i.e. maternal *versus* fetal) of the obstetrical dilemma. All are therefore important to understand the interplay between sex-specific and non-sex-specific selection pressures, fetal and maternal plastic responses to variation in ecological conditions, energetic constraints, and developmental pathways that channel pelvic variability in specific directions.

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